# Snout proportions in some Eurasian hipparions (Mammalia, Equidae): taxonomic and functional implications

**Ann FORSTEN**
Finnish Museum of Natural History,
PB 17, FIN-00014 Helsinki (Finland)
ann.forsten@helsinki.fi

Forsten A. 1999. — Snout proportions in some Eurasian hipparions (Mammalia, Equidae): taxonomic and functional implications. *Geodiversitas* 21 (2) : 255-278.

## ABSTRACT

In the hipparions, length and breadth of the snout and depth of the nasal opening are not well correlated with one another, nor with the shape and placement of the preorbital fossa, recently considered taxonomically important in these equids. These characters are distributed in a mosaic-like fashion among species, making species differentiation and phylogenetic reconstruction difficult.

**KEY WORDS**
hipparions,
snout proportions,
phylogeny,
function.

## RÉSUMÉ

*Les proportions du museau chez quelques hipparions (Mammalia, Equidae) d'Eurasie : implications taxonomiques et fonctionnelles.*

Chez les hipparions, la longueur et la largeur du museau ainsi que la profondeur de la fosse préorbitaire ne sont pas clairement correlées entre elles, ni même avec la forme et la position de cette fosse. Pourtant la valeur de ces mesures a été récemment considérée comme ayant une signification taxonomique importante chez ces équidés. Ces caractères suivent une distribution en mosaïque, au sein des différentes espèces considérées, et leur utilité tant pour la différenciation spécifique des hipparions que pour leur analyse phylogénétique est restreinte.

**MOTS CLÉS**
hipparions,
proportions du museau,
phylogénie,
implications fonctionnelles.

## INTRODUCTION

While the preorbital fossa of the cheek has recently been given great weight in hipparion taxonomy, even used for delimiting "supraspecific groups", the proportions and structure of the snout and the nasal opening have largely been ignored. Complete skulls of *Hipparion* de Christol, 1832, are rare. Most often the snout and/or the cranium are broken off, leaving the middle part of the skull with the cheeks, tooth rows and orbits preserved. Thus there is much less data on the snout of *Hipparion* than on the preorbital fossa of the cheek.

The function of the fossa in *Hipparion* is still unsolved, although there are several alternative hypotheses (see discussion in Sefve 1927: 67-78). In recent equids the shallow fossae serve as attachment areas for levator muscles of the upper lip (Ellenberger & Baum 1943; Zhegallo 1978); the very mobile lips function together with the incisors in gathering food. The extension of the nasal opening in *Hipparion* may reflect the development of the nasal diverticulae, in recent equids situated within the nasal opening (Ellenberger & Baum 1943; but see Gregory 1920).

The shape of the snout in fossil and extant herbivores has recently been debated (e.g. Bunnell & Gillingham 1985; Solounias & Moelleken 1993; Dompierre & Churcher 1996; Eisenmann 1998) and there have been attempts to interprete it ecologically. The shape of the snout is believed to be dictated by the mode of feeding. A broad, anteriorly flattened snout is interpreted as indicating grazing or the unselective gathering of food near the ground. A narrow snout, with the incisors in a sharp arc, is interpreted as indicating browsing or the selective gathering of food at different heights (for the illustration of equid snouts of different breadth, see Eisenmann 1998, fig. 5: 1-10).

In an earlier paper, I (Forsten 1983) discussed the variation in the placement and shape of the preorbital fossa in some Old World *Hipparion*. In the present paper I will describe, compare and discuss the snout and the nasal opening. Old World hipparions group into broad- and narrow-snouted taxa, but with many intermediates. There is weak correspondence with groups delimited on the basis of the preorbital fossa. Also snout proportions and nasal opening extension are only weakly correlated. How should these characters be evaluated and weighted taxonomically and phylogenetically?

## METHODS

In the upper jaw, snout length was measured as the distance from the prosthion (I1-I1) to the middle of a line uniting the anterior tips of P2 (Gromova 1952, table I, skull measure 18); snout width was measured as the outer distance behind I3-I3 (Gromova's measure 40). The nasal opening is the distance anteriorly from between the premaxillae (not including the upper symphysis) posteriorly to where the nasals and premaxillae/maxillae meet (Gromova's measure 28). Skull length, since seldom measureable, was here substituted by the distance P2-anterior rim of orbit (Gromova's measure 11), which is roughly correlated with basal length.

In the lower jaw snout breadth was measured as the outer distance behind i3-i3 (Gromova 1952: table IV, measure 14) and symphysial length anteriorly from between i1-i1 posteriorly to the symphysial notch (Gromova's measure 11).

Relative snout width is expressed in scatter diagrams, plotting maxillar snout width to snout length and mandibular snout width to symphysial length, respectively. Snout length is related to skull length by plotting it to the distance P2-orbit. Nasal opening length is expressed both as an absolute measure and in relation to the tooth row. The preorbital fossa is discussed in terms as in Forsten (1983). I calculated 95% equiprobability ellipses on the data of *H. schlosseri-dietrichi* from Samos Q1 and Samos without more exact locality data and of *H. moldavicum* Gromova, 1952 from Taraklia and Novoelizavetovka, using metrical data, then used the ellipses as models in the diagrams. I did not plot the specimens used for calculating the ellipses, but type specimens are plotted in bold letter abbreviations.

The materials used and the institutes in which are kept the materials seen are listed in the Appendix.

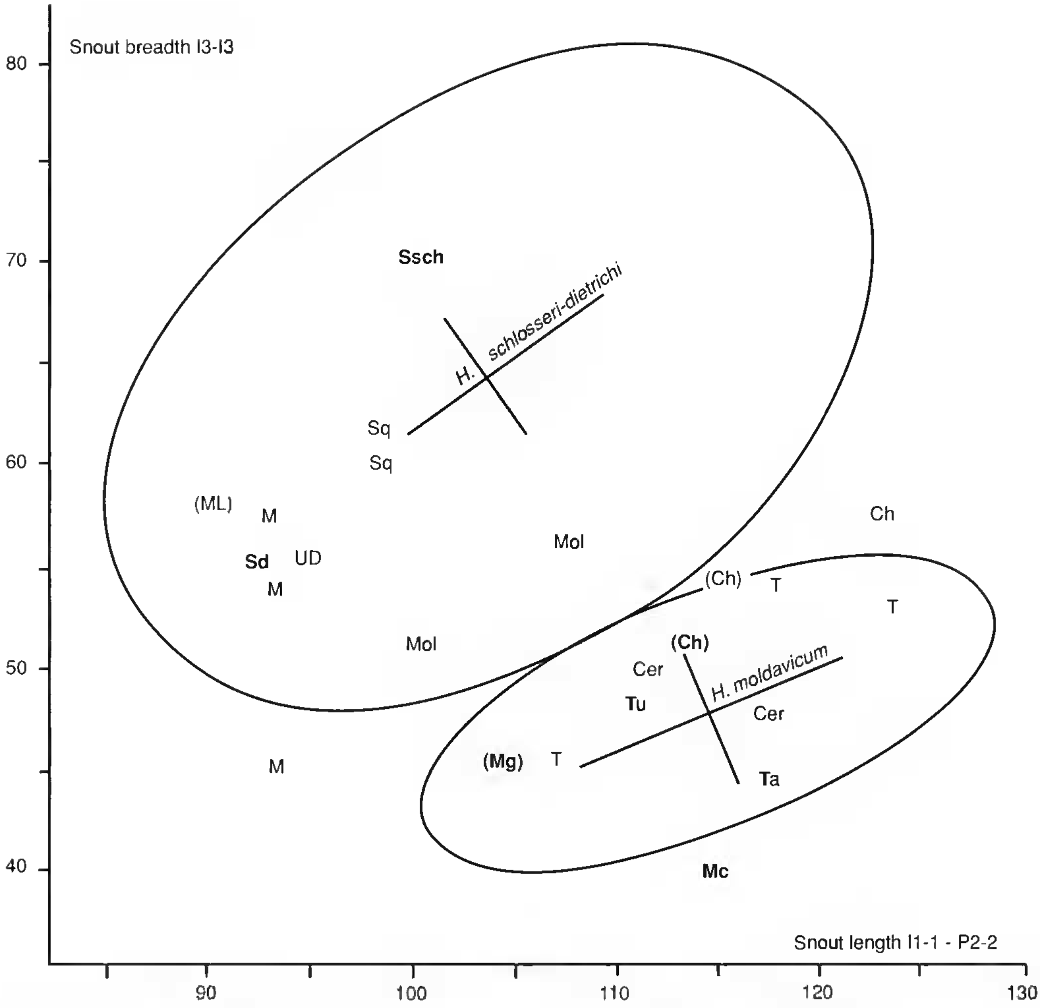

FIG. 1. — Upper snout breadth plotted to snout length in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens from the localities: **Cer**, Cherevichnoe; **Ch**, Chimislia; **K**, Karaslari; **M**, Maragheh; **ML**. Mt. Luberon; **Mol**, Molayan; **Sq**. Saloniki (coll. Arambourg & Puyhaubert); **T**, Tchobruchi; **Tu**, Tudorovo; **UD**, Umen Dol. Bold type abbreviations in figure depict type specimens: **Ch**, *H. pregiganteum* (Chisnau 4040/84); **Mc**, *H. campbelli* (Univ. California Riverside No. 13/1342); **Mg**, *H. gettyi* (Wien No. 840); **Sd**, *H. dietrichi* (Münster S I/7); **Ssch**, *H. schlosseri* (Wien 1911 V 114); **Ta**, *H. moldavicum* (Moscow PIN 1256-3639); **Tu**, *H. tudorovense* (OGUM 1780). Observations in parentheses approximative.

## DESCRIPTION

### EUROPE AND THE NEAR EAST

*Hipparions with a short and/or broad snout*

*Hipparion prostylum* Gervais, 1849 [localities: Mt. Luberon, France; Saloniki, Greece; Karaslari and Umen Dol, Macedonia (former Yugoslavia); possibly Maragheh, Iran], *H. schlosseri-dietrichi* Antonius, 1919-(Wehrli, 1941) [Samos without exact locality (Sondaar 1971, pl. II: a); Samos Q1, Q4, Q6 (Sondaar 1971, pl. II: b); Vathylakkos, Prochoma-1, Ravin des Zouaves (Koufos 1987, fig. 3), Greece; Basiboz (Forsten & Garevski 1989, photos 3, 4), Macedonia; and Maragheh] have a short and broad snout (Fig. 1: upper ellipse). The snout is short also in relation

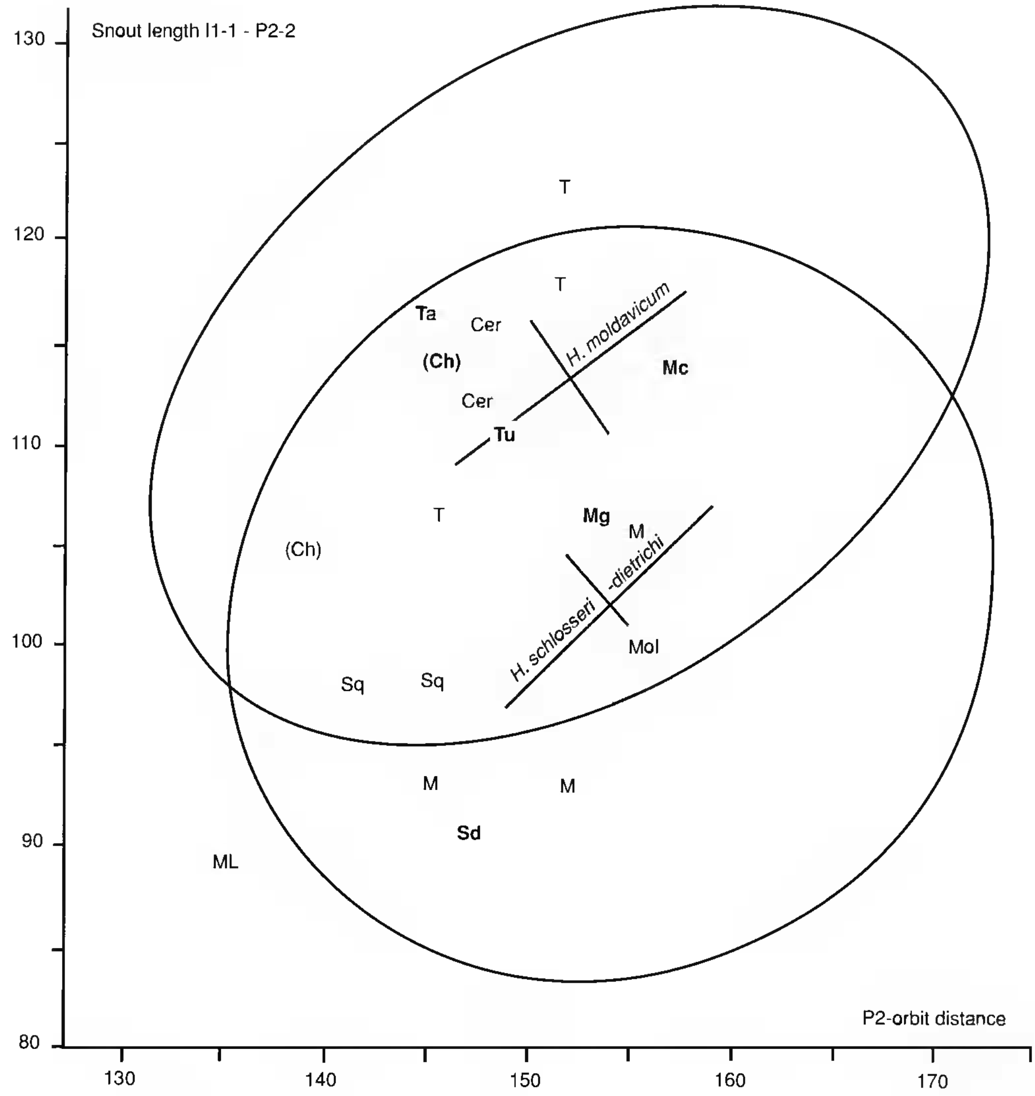

FIG. 2. — Upper snout length plotted to P2-orbit distance in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens from: **Cer**, Cerevichnoe; **Ch**, Chimislia; **M**, Maragheh; **ML**, Mt. Luberon; **Mol**, Molayan; **Sq**, Saloniki; **T**, Tchobruchi. Bold type abbreviations in figure depict type specimens: **Ch**, *H. pregiganteum*; **Mc**, *H. campbelli*; **Mg**, *H. gettyi*; **Sd**, *H. dietrichi*; **Ta**, *H. moldavicum*; **Tu**, *H. tudorovense*. Observations in parentheses are approximative.

to skull length (Fig. 2: lower ellipse) and in the lower jaw the snout is broad in relation to the length of the symphysis (Fig. 3: upper ellipse). The single preorbital fossa of the skull is placed rather far in front of the orbit. It may be faintly delimited and shallow or well-defined, in either case more or less pocketed. There is no clear difference in skull morphology between the smaller specimens (e.g. *H. prostylum* and the holotype of *H. dietrichi*, Münster SI/7) and the larger ones

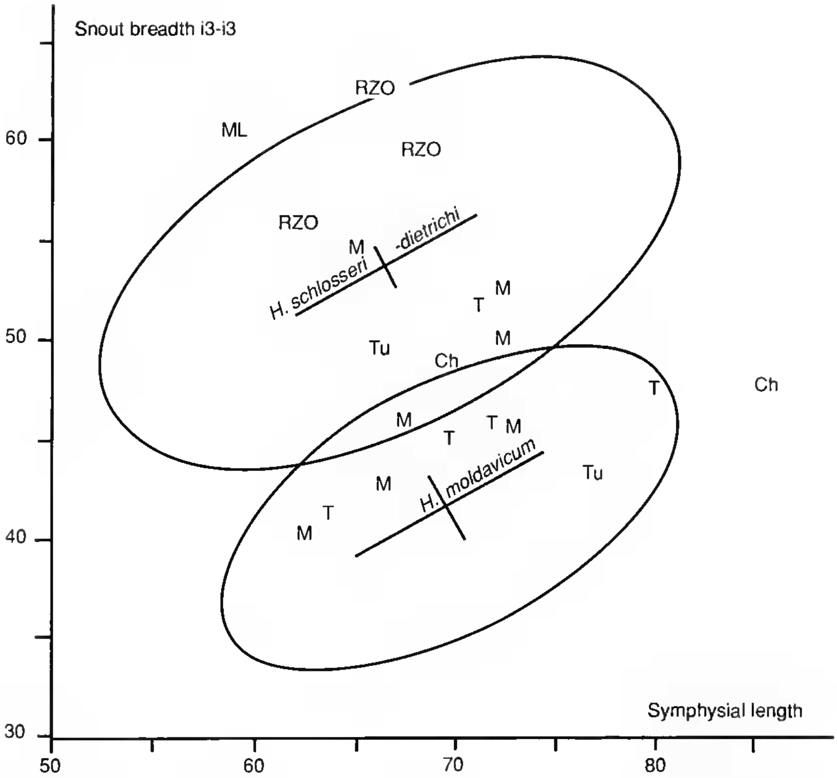

Fig. 3. — Lower snout breadth plotted to symphysial length in European hipparion jaws; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens from: **Ch**, Chimislia; **M**, Maragheh; **ML**, Mt. Luberon; **RZO**, Ravin des Zouaves; **T**, Tchobruchi; **Tu**, Tudorovo.

(e.g. Wien 1911 V 114, the holotype of *H. schlosseri*, and Budapest No. 274) (Figs 1, 2: ML, and in bold: Sd, Ssch). The names *schlosseri* and *dietrichi* were given the same species; although Antonius' name "*schlosseri*" is older, there is some uncertainty as to its validity (inadequate description and illustration of the type). Until the question as to the correct name is solved, I use both united by a hyphen: *H. schlosseri-dietrichi*.

In this group also belongs *H. molayanense* Zouhri, 1992 described from Molayan, Afghanistan (Zouhri 1992). In the two skulls seen, the snout is short, but not as broad as in the former group (Zouhri 1996, pl. 59) (Figs 1, 2: Mol). The preorbital fossa resembles that of the former group in being shallow, oval-egg-shaped, and situated far in front of the orbit.

The above mentioned short- and broad-snouted hipparions, *H. prostylum*, *H. schlosseri-dietrichi*, and *H. molayanense*, also have a short nasal opening, anteriorly either blunt or softly pointed, ending at a level well in front of P2. The nasal opening is short also compared with snout and skull length, except in Paris Mol. 040 from Molayan.

Among the skulls with a short-broad snout fall the type and the referred specimen of *H. garedzicum* Gabuniya, 1959 from Udabno, Georgia (Fig. 4: U, in bold). The nasal opening is short, ending at a level in front of P2 but the preorbital fossa is well-defined and deep (see Gabuniya 1959, pl. VI: 1). On the other hand, among skulls with a shallow preorbital fossa situated far from the orbit can be mentioned the specimen B-50 from Bazaleti, Georgia, referred to as

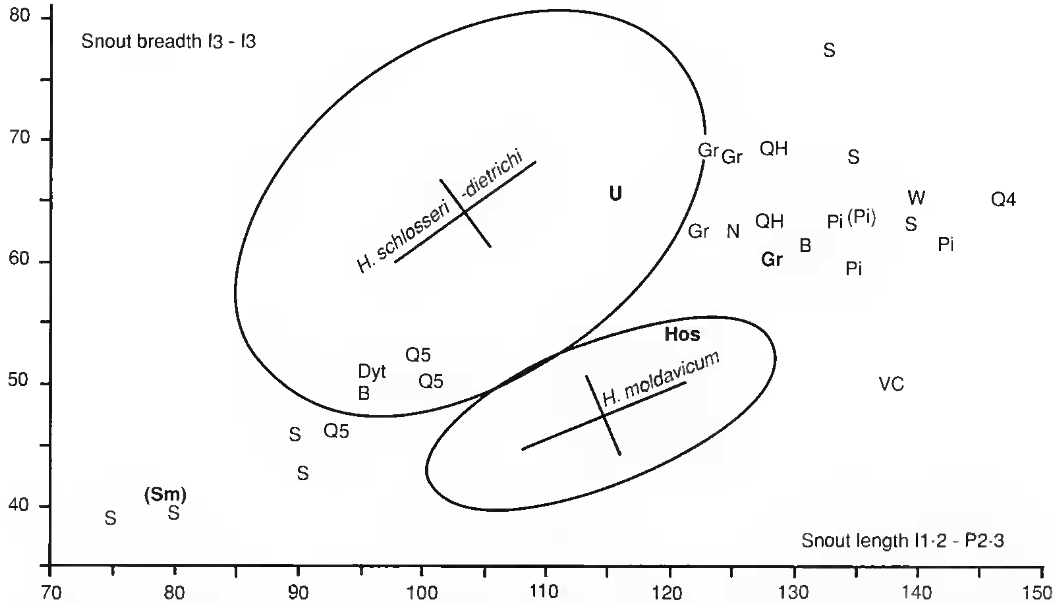

FIG. 4. — Upper snout breadth plotted to snout length in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of *H. matthewi* (scatter to the left) from: **B**, Beluska; **Dyt**, Dytiko (data Koufos 1988, table 1); **Q5**, Samos Q5; **S**, Samos without exact locality. Plotted also hipparions in the *H. primigenium* group (scatter to the right) from: **B**, Beluska; **VC**, Vila de Caballs; **Gr**, Grebeniki; **N**, Nesebr; **QH**, Oued el Hammam; **Pi**, Pikermi; **Q4**, Samos Q4; **S**, Samos without exact locality; **U**, Udabno; **W**, Inzersdorf. Bold type abbreviations in figure depict type specimens: **Gr**, *H. giganteum* (OGUM 1015); **Hos**, *H. catalaunicum* (BMNH 16397); **Sm**, *H. matthewi* (Budapest Ob/557); **U**, *H. garedzicum* (Tbilisi No. 156/13).

*H. garedzicum* by Meladze (1967, table VIII) and as *H. molayanense* by Zouhri (1992, 1996), but which differs from both in the snout being long and narrow (Fig. 5: Bz to the far right in diagram). The type skull of *H. tudorovense* Gabuniya, 1959 (OGUM 1780; Gabuniya 1959, pl. V: 2) from Tudorovo, Moldova, also has a shallow preorbital fossa situated relatively far in front of the orbit, but a narrow snout (Figs 1, 2: Tu, in bold). The nasal opening in B-50 from Bazaleti and OGUM 1780 from Tudorovo ends level with P2. A very fragmentary skull (Inst. of Paleobiology, Tbilisi No. 148/191; Gabuniya 1959, pl. VI: 3) from Kiourtevioul, 50 km north of Lake Urmia, Iran, the holotype of *H. urmiense* Gabuniya, 1959 has a shallow and faint fossa and a nasal opening extending level with P2-P3. Since the snout is lacking and the orbits are not visible, the placement of the preorbital fossa in relation to the orbit and the snout proportions are unknown.

A relatively broad snout is characteristic of the skull of *H. matthewi* Abel, 1926 [localities: Samos Q5 (Sondaar 1971, Pl. Ia-b) and Samos without exact locality data (*H. nicosi* Bernor & Tobien, 1989), Ravin de la Pluie, Vathylakkos, and Prochoma-1 (*H. macedonicum* Koufos, 1984; Koufos 1987, fig. 8), Dytiko (*H. matthewi* and *H. periafricanum* Villalta & Crusafont, 1957; Koufos 1987), Saloniki, Greece (coll. Arambourg & Puyhaubert); ?Umen Dol and Beluska, Macedonia; and Ploski Blagoevradsko (*H. microtatou* Nikolov, 1971), Bulgaria] but the relative breadth is less than in the *H. prostylum/schlosseri-dietrichi* group (Figs 4, 6: scatter to the left in diagram). In the lower jaw the snout is medium broad relative to symphysial length (Fig. 7: scatter to the left in diagram). The preorbital fossa in *matthewi* varies from well-defined to almost absent; in some specimens from Q5 it is double, consisting of a posterior fossa proper and an anterior, smaller subnasal fossa (Forsten

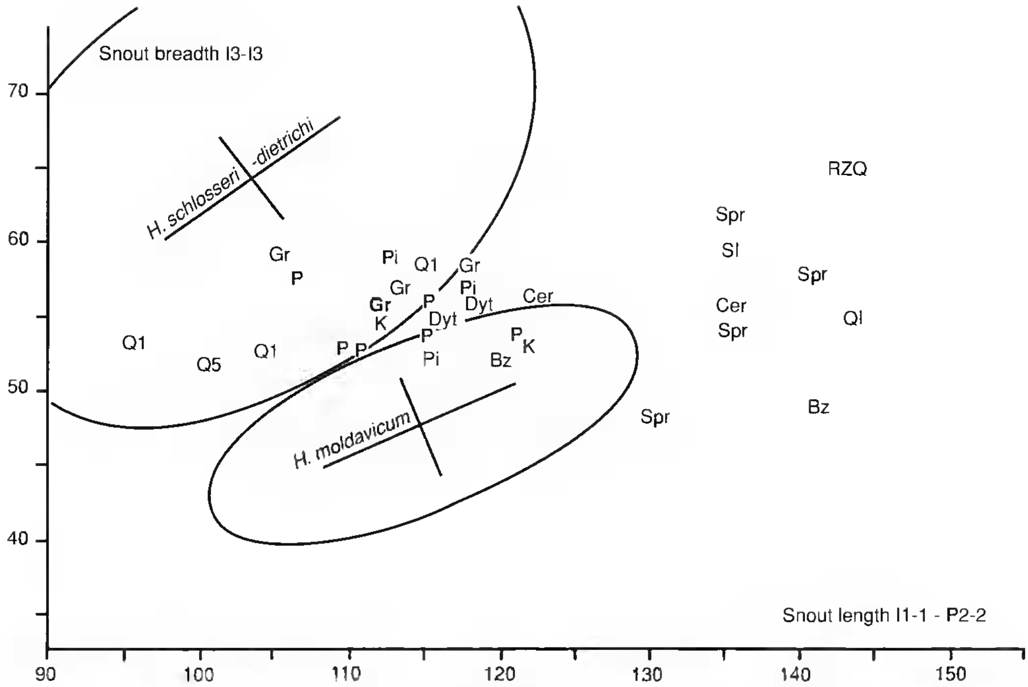

Fig. 5. — Upper snout breadth plotted to snout length in European hipparions; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality data) and *H. moldavicum* (Tarakliya and Novoelizavetovka) Plotted are specimens of: *Hipparion verae* (**Gr**, Grebeniki; **K**, Karaslari ); *H. mediterraneum* [**Bz**, Bazaleti (specimen B-51 to the left in diagram); **Dyt**, Dytiko (data Koufos 1988, table 1); **Pi**, Pikermi (data partly Koufos 1987, table 1)]; *Hipparion* sp. with a double fossa (**Q1** and **?Q5**, Samos quarries); *Hipparion* sp. (**P**, Piera). Plotted are also skulls of *H. proboscideum* (scatter to the right in diagram) from: **Cer**, Cherevichnoe; **RZO**, Ravin des Zouaves; **Spr**, **Sl** and **Q1**, Samos quarries. The skull B-50 from Bazaleti with a weak fossa falls in among the specimens of *H. proboscideum*. Bold type abbreviation in figure depicts type: **Gr**, *H. verae* (OGUM 1016).

1983). The nasal opening in *H. matthewi*, like snout length, varies from short to long or from a level 1 cm in front of P2 to level with P3 parastyle. The fragmentary nasal opening in München 1899 VII 31b (*H. nicosi* holotype) from Samos extends level with P2 and is thus comparable to the holotype of *matthewi* (Budapest OK/557), also from Samos. In the rather long-snouted specimens with a double fossa from Samos Q5, the nasal opening is long.

The skulls of *H. matthewi* from Q5 resemble some larger skulls with a double fossa found from Samos Q1-Andriano (see Forsten 1983, fig. 3), possibly also from Samos Q5 and Gülpinar, Turkey (Figs 5, 8: Q1, Q5); they are here referred to as *H.* sp. (with a double fossa). They have a relatively short-broad snout and the nasal opening ends level with P2, but both the snout and the nasal opening are longer in relation to skull and snout length, respectively, than in *H. schlosseri-dietrichi* of similar size and from the same localities. This unnamed taxon seems to be related to the hipparions in the *H. mediterraneum* (Roth & Wagner, 1855) group, in which the fossa is situated close to the orbit, but is rarely double. The proportions of the snout and the depth of the nasal opening in these specimens from Samos are like in *H. mediterraneum* from Pikermi, Greece, but relatively broader and deeper, respectively, than in the various local forms of *H. moldavicum* Gromova, 1952 from Moldova and Ukraine, belonging in the same species group.

### *Hipparions with a long snout and/or nasal opening*

Extreme for its long and narrow snout among

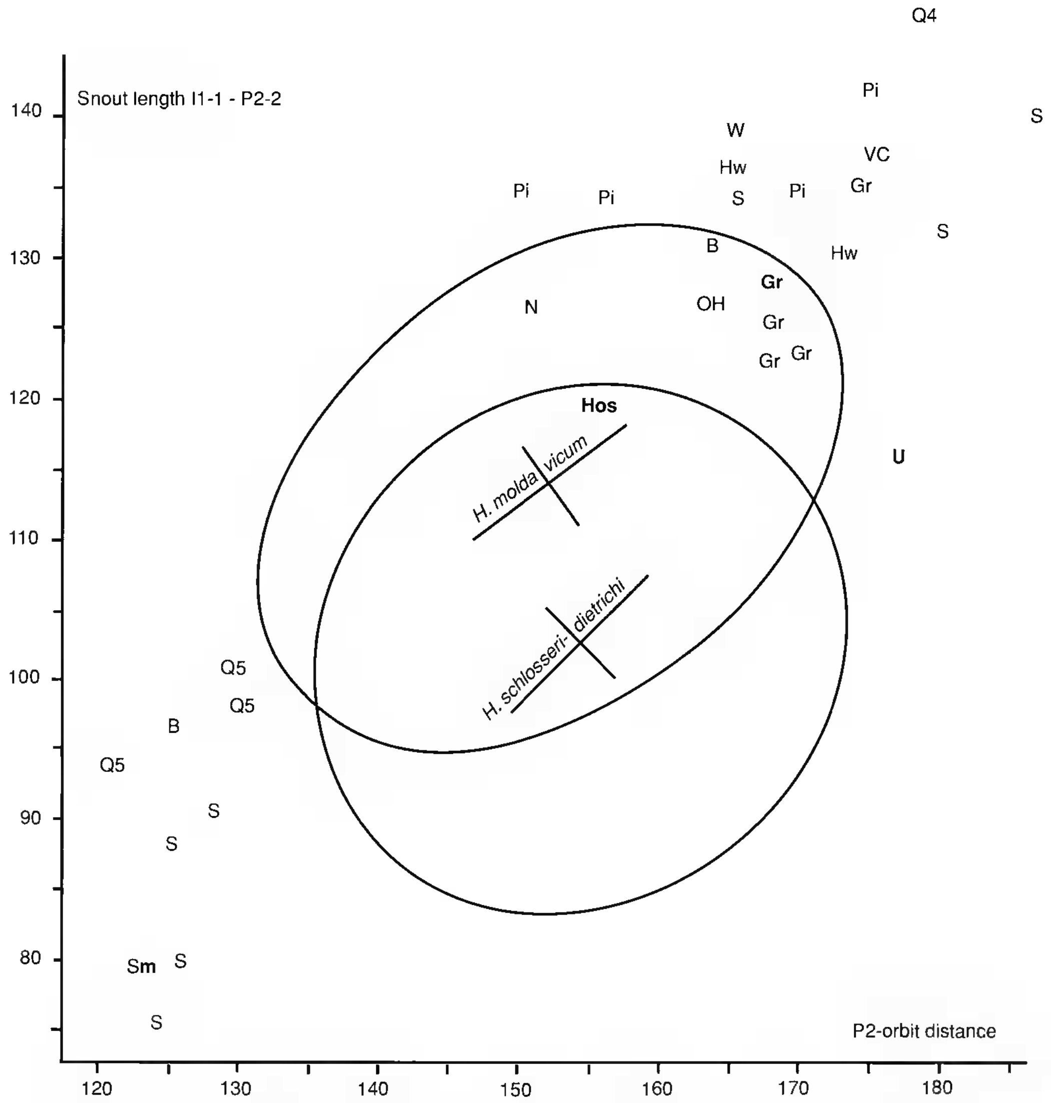

FIG. 6. — Upper snout length plotted to P2-orbit distance in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of *H. matthewi* (scatter to the left in diagram) from: **B**, Belushka, **Q5** and **S**, Samos quarries. Plotted are also specimens of the *H. primigenium* group (scatter to the right) from: **B**, Beluska; **Gr**, Grebeniki; **Hos**, Hostalets; **Hw**, Höwenegg; **N**, Nesebr; **OH**, Oued el Hammam; **Pi**, Pikermi; **Q4** and **S**, Samos quarries; **U**, Udabno; **VC**, Vila de Caballs; **W**, Inzersdorf. Bold type abbreviations in figure depict type specimens: **Gr**, *H. giganteum*; **Hos**, *H. catalaunicum*; **Sm**, *H. matthewi*; **U**, *H. garedzicum*.

the European hipparions is the specimen B-50 from Bazaleti with a shallow fossa (Meladze 1967, table VIII) (Figs 5, 8: Bz to the far right and top centre in diagram). Specimen B-51 from the same locality, but with a maximally developed, double preorbital fossa, has a medium long snout similar in its breadth: length proportions to that in *H. moldavicum* (Meladze 1967, table VII) (Figs 5, 8: Bz in centre of diagram). In both specimens the snout is longer than in *H. mediterraneum*, and in the lower jaw (Meladze 1967, table IX) the symphysis is longer and the

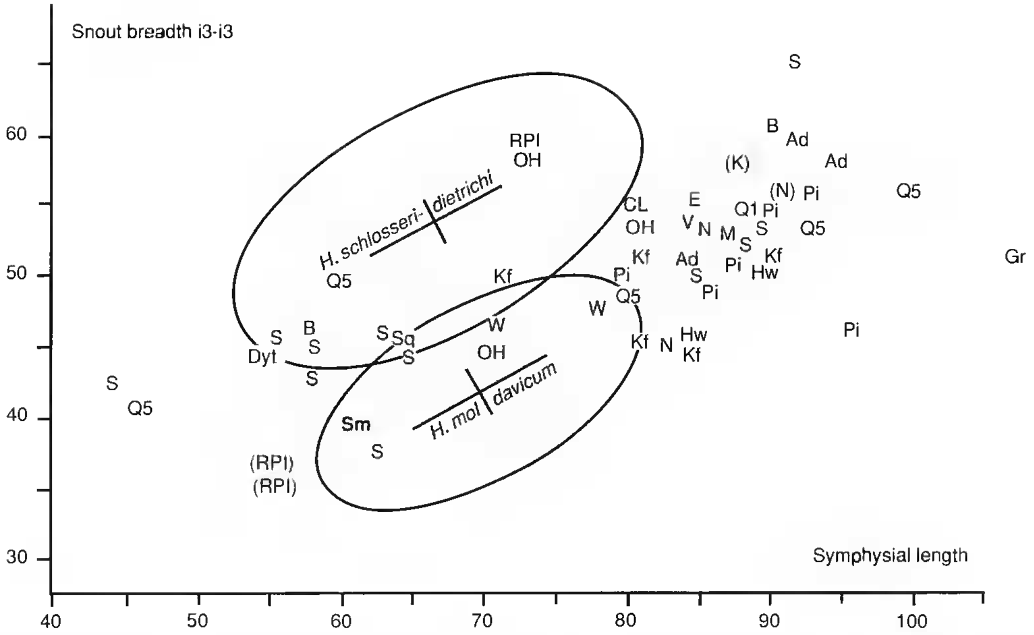

FIG. 7. — Lower snout breadth plotted to symphysial length in European hipparion jaws; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of *H. matthewi* (scatter to the left) from: **B**, Beluska; **Dyt**, Dytiko (data Koufos 1988, table 2); **Q5** and **S**, Samos quarries; **RPl**, Ravin de la Pluie; **Sq**, Saloniki. Plotted are also (scatter to the right in diagram) not separable specimens of hipparions of the *H. primigenium* group and *H. proboscideum* from: **Ad**, **S**, **Q1** and **Q5**, Samos quarries; **B**, Beluska; **CL**, Can Llobateres; **E**, Eppelsheim; **Gr**, Grebeniki; **K**, Karaslari; **Kf**, Kalta; **M**, Maragheh; **N**, Nesebr; **OH**, Oued el Hammam; **Pi**, Pikermi; **RPl**, Ravin de la Pluie; **V**, Vozarzi; **W**, Inzersdorf and Wienerberg. Bold type abbreviations in figure depict type specimens: **Sm**, *H. matthewi*. Observations in parentheses are approximative.

snout narrower (Fig. 9: Bz). Compared for their nasal opening depth, that in B-50 is absolutely shorter than in B-51, but in both specimens the nasal opening reaches level with P2.

*Hipparion* sp. from Piera, Spain, has a well-defined, pocketed, pear-shaped to rounded triangular preorbital fossa and a long snout in relation to skull length (Forsten 1968, pl. 2) (Figs 5, 8: P). For its breadth, the snout resembles that in *H. mediterraneum* and *H. verae* Gabuniya, 1959 (Fig. 5: P, Pi, Gr). The nasal opening is short, ending from a level 2 cm in front of P2 to level with P2 paracone; it is short also in relation to snout and skull length.

*Hipparion proboscideum* Studer, 1911 [localities: Samos Q1 and Samos without exact locality data (Studer 1911, figs 1, 3, 4a; Sondaar 1971, pl. IIIa-d), Ravin des Zouaves (Koufos 1987, fig. 3), Greece; Vozarzi and Karaslari, Macedonia (Forsten & Garevski 1989, photos 1, 2); Valea Sarii, Romania (Forsten 1980); Kavakdere, Turkey; and Cherevichnoe, Ukraine, (*H.* sp. cf. *proboscideum* Forsten & Krakhmalnaya, 1997, fig. 7)], with an arrangement of the double preorbital fossa similar to that in specimen B-51, has a narrow snout similar to that in B-50, but the snout is not long in relation to skull length (Figs 5, 8: Spr, S1, Q1, RZO, Cer). The nasal opening is long and deep, extending from level with P2 parastyle to P3 mesostyle. In its snout proportions *H. proboscideum* resembles the second large species from Samos Q1-Andriano and Q4, called *H.* cf. *proboscideum* and *H. primigenium* (v. Meyer, 1829) (Sondaar 1971, pl. III: e; Forsten 1983, in Appendix referred to as *H.* aff. *brachypus* Hensel), in which the single preorbital fossa and nasal opening are as deep as in the former, but in which the snout is longer in relation to skull length and broader than in *H. proboscideum* (Figs 4, 6: S, Q4). This taxon,

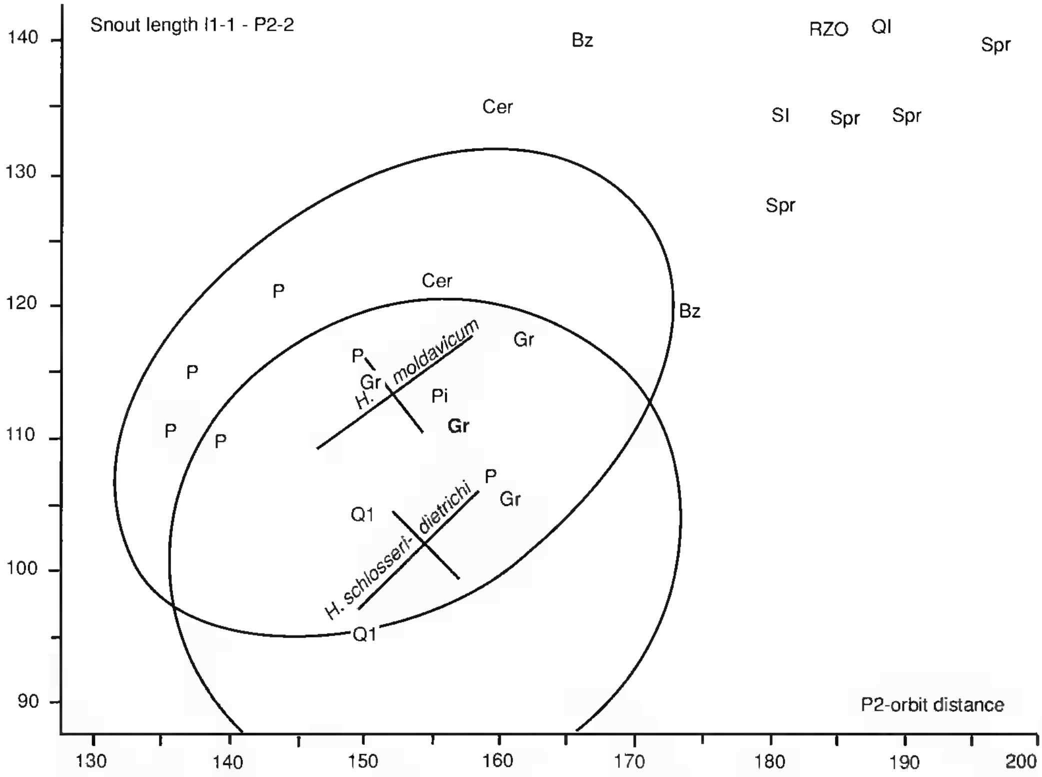

FIG. 8. — Upper snout length plotted to P2-orbit distance in European hipparion skulls; measurements in mm; 95% equiprobability ellipses calculated and drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted are specimens of *H. mediterraneum* [**Bz**, Bazaleti (specimen B-51 in centre of diagram); **Pi**, Pikermi]; *H. verae* (**Gr**, Grebeniki); *Hipparion* sp. with a double fossa (**Q1**, Samos Q1); and *Hipparion* sp. (**P**, Piera). Plotted are also specimens of *H. proboscideum* (scatter to the right) from: **Bz**, Bazaleti (specimen B-50 in top-centre of diagram); **Cer**, Cherevichnoe; **Q1**, **Sl** and **Spr**, Samos quarries; **RZO**, Ravin de Zouaves. Bold type abbreviation in figure depicts type: **Gr**, *H. verae*.

similar to the large one from Pikermi (*H. brachypus* Hensel, 1862, see Koufos 1987: pl. III) (Figs 4, 6: Pi), leads over to hipparions with a mostly long snout, comprising the *H. mediterraneum* and the *H. primigenium* species groups.

*Hipparions with a medium long and narrow snout*
A medium long and narrow snout characterizes the local samples of *H. moldavicum* [localities: Tarakliya, Novoelizavetovka, Tudorovo, Chimishlia, Cherevichnoe, and Chiobruchi, Ukraine and Moldova, possibly Maragheh, Iran) (Gromova 1952, tables I-III; Gabuniya 1959, pls III: 2, 3, IV: 1, 2; Watabe & Nakaya 1991; Forsten & Krakhmalnaya 1997, fig. 6) (Figs 1, 2: lower and upper ellipse, respectively)]. The nasal opening extends from a level 1 cm in front of P2 to P2 mesostyle; it is short in relation to snout and skull length. In the lower jaw the snout is narrow in relation to symphysial length (Fig. 3: lower ellipse). *Hipparion moldavicum* has a well-defined, single preorbital fossa placed close to the orbit, a character which it shares with *H. mediterraneum* from Pikermi, but has a narrower snout and shorter nasal opening even taking into account its smaller skull size. Similar narrow snout proportions are found in skulls from Maragheh, described as *H. gettyi* Bernor, 1985 and *H. campbelli* Bernor, 1985 (Bernor 1985), in OGUM 1780 (type of *H. tudorovense*) from Tudorovo, and in the type skull (Kishinev 4040/84) of *H. praegiganteum* Tarabukin, 1967 from Chimishlia, Moldova (Figs 1, 2: Tu, Mg, Mc, Ch, in bold). The single preorbital fossa of

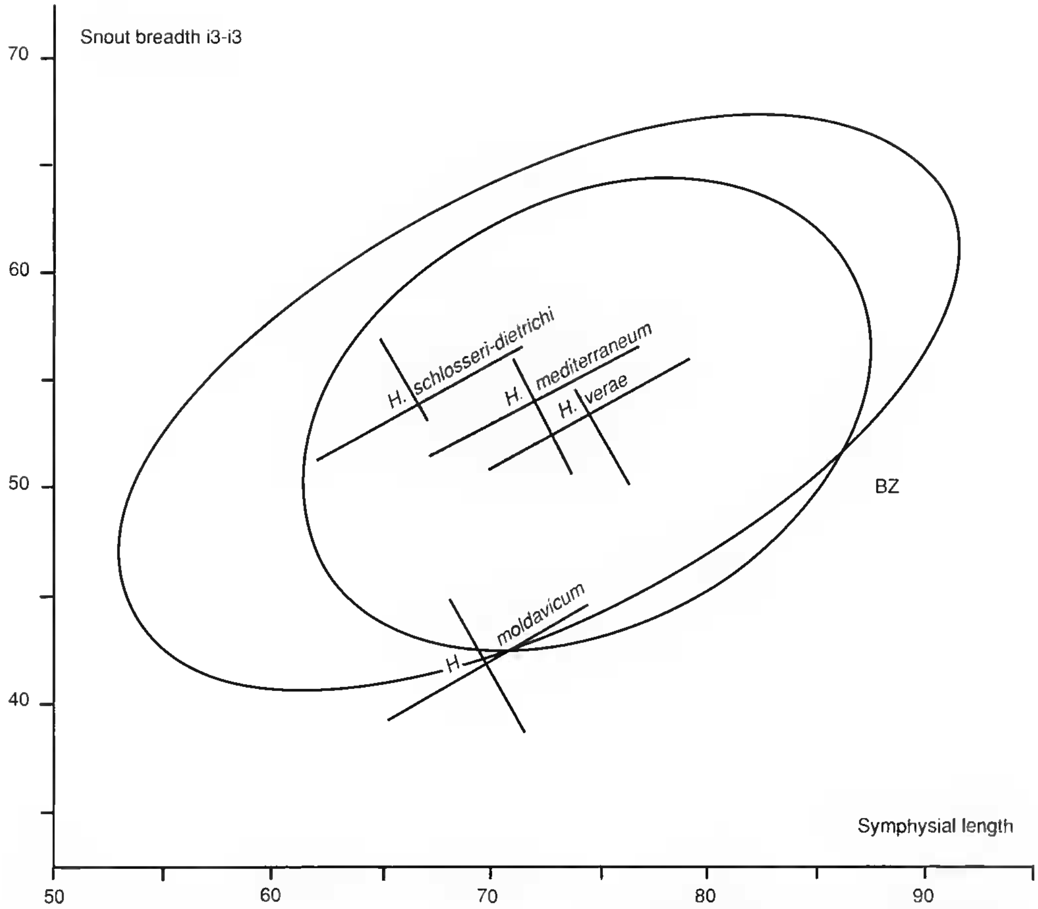

Fig. 9. — Lower snout breadth plotted to symphysial length in European hipparion jaws; measurements in mm; 95% equiprobability ellipses calculated and drawn for *Hipparion mediterraneum* from Pikermi and *H. verae* from Grebeniki. Axes also drawn on the data of *H. schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Plotted is single specimen B-54 jaw from **Bz**, Bazaleti.

these skulls is rounded triangular to oval, shallow or with a posterior pocket, and situated moderately far from the orbit. The nasal opening ends level with P2; it is particularly long in relation to snout and skull length in the type skulls (Wien, No. 8401 and BMNH 44574/cast of Univ. California Riverside No. 13/1342) of *H. gettyi* and *H. campbelli* from Maragheh. *Hipparion gettyi* may be a younger synonym of *H. tudorovense*, with which it shares similar snout proportions and proportions between the orbit-fossa: P2-orbit distances, and similar extension of the nasal opening. *Hipparion campbelli* may be a younger synonym of *H. urmiense*, with which it shares a similar long tooth row and the extension of the nasal opening (see Watabe & Nakaya 1991).

### *Hipparions with a medium long and broad snout*

Although similar in the shape and placement of the preorbital fossa, *H. mediterraneum* (Pikermi and Dytiko, Greece, Koufos 1987, pls I, II; Koufos 1988, pls 1, 2; possibly Maragheh, Iran, and Bazaleti, Georgia) has a broader snout than *H. moldavicum*, although overlapping the latter in snout proportions (Figs 5, 8: Pi, Dyt). The nasal opening is deeper, reaching level with P2, even with P2-P3.

*Hipparion verae* from Grebeniki, Moldova, has

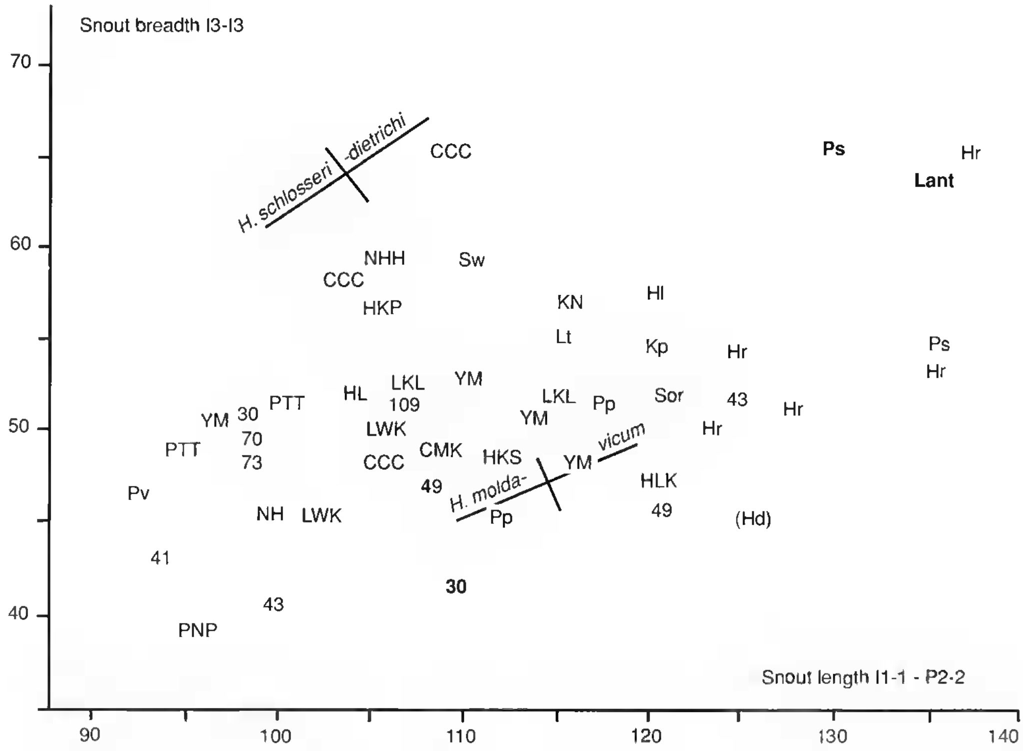

FIG. 10. — Upper snout breadth plotted to snout length in Asiatic hipparions; measurements in mm. For comparison the axes are drawn on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). Abbreviations: **CCC**, Chang Chia Chuang and 2 miles W of Chang Chia Chuang; **CMK**, Ch'eng Chia Mao Kou; **Hd**, *Hipparion dermatorhinum*; **HKP**, Hsiao Ku Po; **HKS**, Hsiao Kou Shan; **Hl**, *H. licenti*; **HL**, Hsi Liang; **HLK**, Huang Lu Kou; **Hr**, *Proboscidipparion rocinantis* (various locations); **KN**, Khirgis Nur; **Kp**, Kalmakpai; **Lant**, Lantian; **LKL**, Lu Kao Ling; **LT**, Ling Tou; **LWK**, Liao Wang Kou; **NH**, Nan Ho; **NHH**, Nan Hao Hsia; **PNP**, Po Niu Po; **Pp**, *P.* "*pater*"; **Ps**, *P. sinense*; **PTT**, Pai Tao Tsun; **Sor**, Sor; **Sw**, Siwaliks; **YM**, Young Mu Kou; **30**, Loc. 30; **43**, Loc. 43; **44**, Loc. 44; **49**, Loc. 49; **70**, Loc. 70; **73**, Loc. 73; **109**, Loc. 109. Bold type abbreviations in figure depict the types: **49**, *H. plocodus* Sefve, 1927 (Uppsala No. 3824), **30**, *H. fossatum* Sefve, 1927 (Uppsala No. 3821), **Lant**, *H. weihoense* Liu, Li & Zhai, 1978 (IVPP V 3113.1); **Ps**, *Proboscidipparion sinense* Sefve (Uppsala No. 3925 & 3926).

snout proportions resembling those of *H. mediterraneum* (Gabuniya 1959, pls II: 1, 3, III: 1, VIII: 2) (Figs 5, 8: Gr, Pi). In the lower jaw of both forms the snout is broad in relation to the length of the symphysis (Fig. 9: Gr, Pi), even resembling the jaws of the *H. prostylum/schlosseri-dietrichi* complex. *Hipparion verae* has a differently shaped and placed preorbital fossa and the nasal opening is shallower than in *H. mediterraneum*, reaching from a level 2-1 cm in front of P2 to P2 mesostyle. Like in the latter, the preorbital fossa is occasionally double.

In skulls from Basiboz, Umen Dol and Karaslari (Macedonia, former Yugoslavia), referred to as *H. verae* in Forsten & Garevski (1989, photos 5-7), the preorbital fossa spills into the fossa buccinator, in some cases forming an isolated, anterior subnasal fossa level with P2. In these specimens the placement, shape and depth of the preorbital fossa varies, as does the depth of the nasal opening (ending from 1 cm in front of P2 to level with P2 paracone). The snout is medium broad in two measureable specimens (PMM Kar 86/73 and Kar 203/73), belonging either to this species or to *H. prostylum/schlosseri-dietrichi* (Fig. 5: K).

### *Hipparions lacking a preorbital fossa*

The earliest known *Hipparion* in Europe lacking

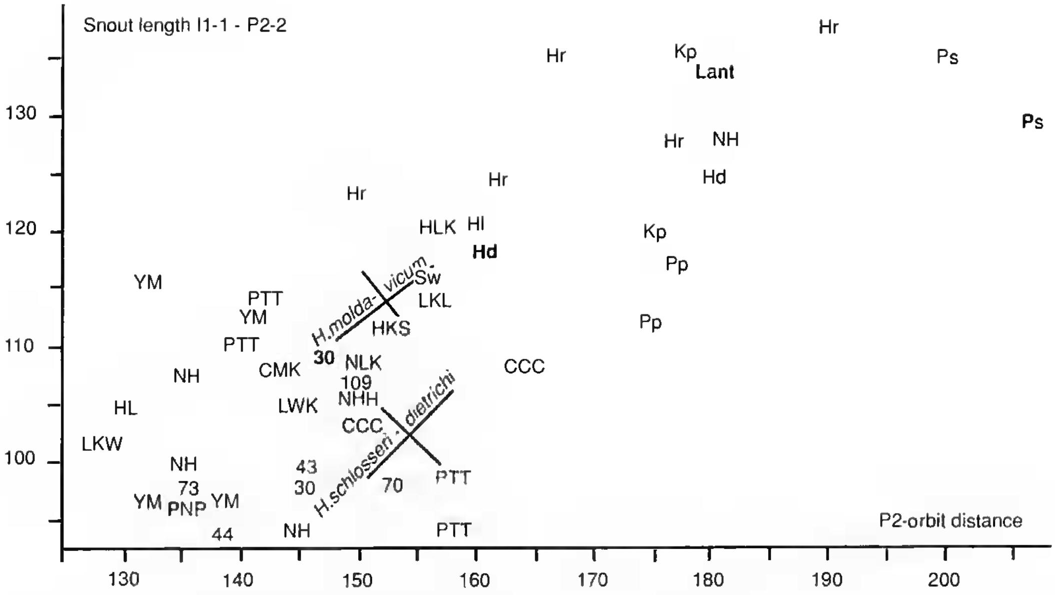

FIG. 11. — Upper snout length plotted to P2-orbit distance in Asiatic hipparions; measurements in mm. For comparison are drawn the axes calculated on the data of *Hipparion schlosseri-dietrichi* (Samos Q1-Andriano and Samos without exact locality) and *H. moldavicum* (Tarakliya and Novoelizavetovka). For abbreviations see Figure 10. Bold type abbreviations in figure depict types: **Hd**, *H. dermatorhinum* (Uppsala No. 3872); **Lant**, *Hipparion weihoensis*; **Ps**, *Proboscidipparion sinense*; **30**, *H. fossatum*.

a preorbital fossa is *H. platygenys* Gromova, 1952 from the Meotian of Tarakliya (Gromova 1952, table IV). Its upper snout is unknown, but in three lower snouts the symphysis is long and the snout medium broad in the measureable specimens. Gromova (1952) referred the specimen PIN 1256-3634 to *H.* sp. or *H. platygenys*. *Hipparion platygenys* may be a junior synonym of *H. hippidiodus* Sefve, 1927 from China (see below).

From the Pliocene is known *Proboscidipparion rocinantis* (Hernandez-Pacheco) from Villaroya, Spain, and Kvabebi, Georgia, lacking or with a faintly defined preorbital fossa. This species represents the dentally advanced caballoid hipparions, referable to a genus of their own: *Proboscidipparion* Sefve, 1927 (Forsten 1997). The snout of the skull and jaws from Villaroya is long and medium broad; that of the skull from Kvabebi (Vekua 1972, Ris. 27-28, tables XVIII, XIX) is short and broad. The nasal opening is short, ending in front of or level with P2, respectively. *Proboscidipparion rocinantis* is also found in China and Mongolia, where specimens tend to have a narrow snout (see below).

### *The* Hipparion primigenium *group*

Among the early (Vallesian) forms of this group represented by skulls with snouts are the hipparions from Vila de Caballs and Hostalets, Spain (*H. catalaunicum* Pirlot, 1956; Pirlot 1956, pl. V); Höwenegg, Germany; Inzersdorf, Austria; Nesebr, Bulgaria (*H. presulcatum* Nikolov, 1971 and *H. nesebricum* Bakalov & Nikolov, 1962; Nikolov 1971, table I: 1, 1a); Kalfa and Braila, Moldova (*H. sarmaticum* Lungu, 1973; Lungu 1973, Ris. 1, table I); and Oued el Hammam, Algeria (*H. africanum* Arambourg, 1959); later (Turolian) forms are found at Udabno, Georgia (*H. garedzicum* Gabuniya, 1959, pl. VI: 1); Samos Q1-Andriano and Q4 (*H.* cf. *proboscideum* Sondaar 1971, pl. IIIe; here *H.* aff. *brachypus*), Pikermi (*H. brachypus* Koufos, 1987, pl. III), and Grebeniki (*H. giganteum* Gromova, 1952, table XII), evidently also at Beluska, Karaslari, and Vozarzi, Macedonia. While the early forms have a triangular or oval fossa, in the later forms the fossa is pear-shaped. The snout is long and broad (Figs 4, 6), but the length of the nasal opening varies considerably between the local samples. It is very shallow in the specimens

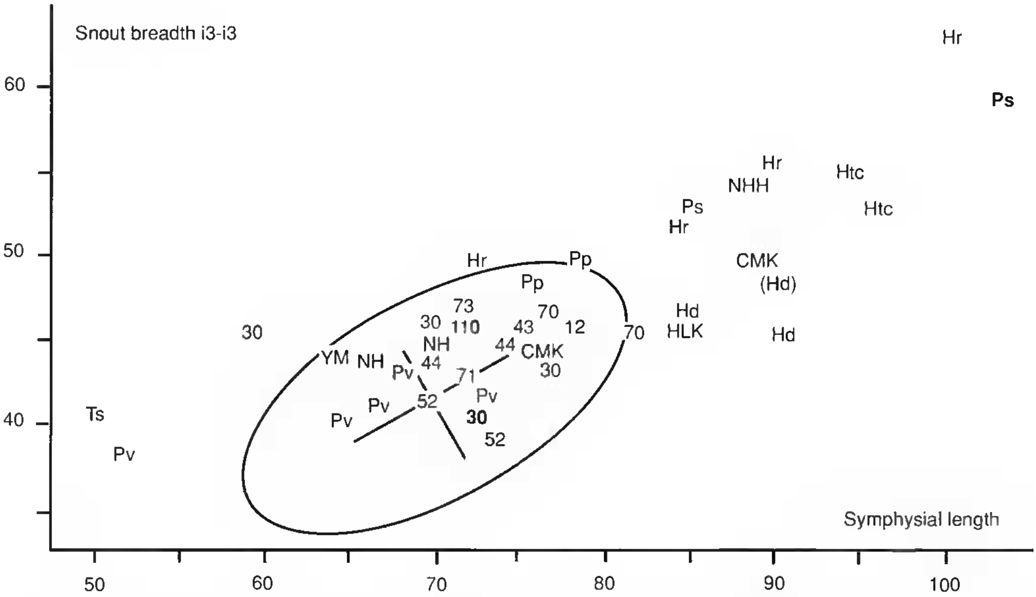

FIG. 12. — Lower snout breadth plotted to symphysial length in Asiatic hipparion jaws; measurements in mm. Abbreviations as in Figure 10, in addition to **Htc**, *Hipparion tchicoicum*; **Ts**, Tan Tsun; **12**, Loc. 12; **52**, Loc. 52; **71**, Loc. 71; **110**, Loc. 110. Bold type abbreviations in figure depict types: **Ps**, *Proboscidipparion sinense*; **30**, *Hipparion fossatum*.

from Hostalets (ending 3 cm in front of P2), Inzersdorf (3-2 cm), Kalfa (2-1 cm), Höwenegg (3-1 cm), Udabno and Grebeniki (from 1-2 cm in front of P2 to P2 anterior tip); medium deep from Vila de Caballs (level with P2 anterior tip), Oued el Hammam (just in front of P2 to P2 paracone), and Nesebr (P2 mesostyle); and deep in the skulls from Pikermi (P2 mesostyle-P3 paracone) and Samos Q1-Andriano (level with P3). *Hipparion garedzicum* from Udabno (see above) differs from the rest of the group in having a short snout relative to skull length (Figs 4, 6: U, in bold).

In the lower jaw the snout is broad in two (MNHN 89, 143), narrow in a third (MNHN 98) of the jaws from Oued el Hammam; it is also broad in the jaw (Univ. Thessaloniki, RPl-1) from Ravin de la Pluie, Greece, referred to as *H. primigenium* (Koufos 1986), and from Can Llobateres (Fig. 7: OH, RPl, CL). In the other local samples in this group the lower snout tends to be narrow and the symphysis long, particularly in the large forms from Pikermi, Samos, and Grebeniki.

## ASIA

### *Hipparions with a short and broad snout*

There are few hipparions in Asia with as pronouncedly short and broad a snout as the members of the *H. prostylum/schlosseri-dietrichi* group. Most Asiatic hipparions, e.g. all the Chinese species kept in Uppsala described by Sefve (1927) and the majority of the specimens in the AMNH, have a narrow snout (Figs 10, 12). As for snout length in relation to the distance P2-orbit, there are both long and short-snouted forms (Fig. 11). The conformation of the nasal opening and the nasals show great variation among the finds, as does the preorbital fossa.

A skull (New York, AMNH 19761) from 0.5 mile south-west of Dhok Pathan, Pakistan, called *H. antelopinum* Falconer & Cautley, 1847 (Matthew 1929), has a medium long but broad snout (Figs 10, 11: Sw) and a small, although posteriorly deep, preorbital fossa placed far in front of the orbit. The nasal opening ends at a level 1 cm in front of P2 and is short also in relation to snout and skull length. The species represented by this skull seems to be a vicar of the

European-Near Eastern *H. prostylum/schlosseri-dietrichi* group mentioned above.

From Chang Chia Chuang, Shanxi, China, there are two skulls (AMNH 44-B 421 juv. and 44-B 427) in which the snout is quite broad (Fig. 10: CCC). The preorbital fossa, situated far from the orbit, is small and oval-pearshaped; the nasal opening appears short. From 2 miles west of Chang Chia Chuang, there are two skulls (AMNH 21-B 38 and 25-B 49), the one with a broad, the other with a narrow snout (Fig. 10: CCC); the snout is also short in relation to skull length (Fig. 11: CCC). The nasal opening is anteriorly pointed and deep, extending level with P2 metacone-P3 mesostyle. The deep fossa is situated close to the orbit. Of these skulls, AMNH 21-B 38 with a nasal opening extending level with P3 mesostyle, resembles the peculiar Chinese *H. licenti* Qiu, Huang & Guo, 1987 (Qiu *et al.* 1987, pls IX, XII) (Beijing, IVPP THP 20764, 20767, 20769 juv. and London, BMNH 44577/cast of F:AM 125708), characterized by its strongly retracted nasal opening, reaching level with M1 mesostyle, but evidently unreduced nasals. The snout in *H. licenti* is known only in BMNH 44577 and is rather long and medium broad (Figs 10, 11: Hl). The preorbital fossa is double, the posterior one situated close to the orbit (Qiu *et al.* 1987, fig. 26).

A skull from Nan Hao Hsia (AMNH 35-B 255) has a medium long and broad upper snout, but the snout of the jaw of the same specimen is narrow (Figs 10-12: NHH). The nasal opening is very short, ending 2 cm in front of P2; the preorbital fossa is pear-shaped. A skull from Hsiao Ku Po (AMNH 53-B 641) resembles the previous one in having a broad snout (Fig. 10: HKP), very short nasal opening, and a pear-shaped preorbital fossa.

*Hipparion elegans* Gromova, 1952 from Pavlodar, Kazakhstan, resembles some *H. matthewi* in having a relatively broad upper snout (Fig. 10: Pv), as well as in the placement and shape of the single preorbital fossa (Gromova 1952, table V; Forsten 1983, fig. 4). The nasal opening seems short, extending from 1 cm in front, to the anterior tip, of P2. The five measureable lower jaws correspond to those of some *H. matthewi* in the snout being narrow (Fig. 12: Pv). This species is an Asiatic vicar of the dwarf *H. matthewi*, from which it differs in the morphology of its teeth and in the proportions of its limb bones.

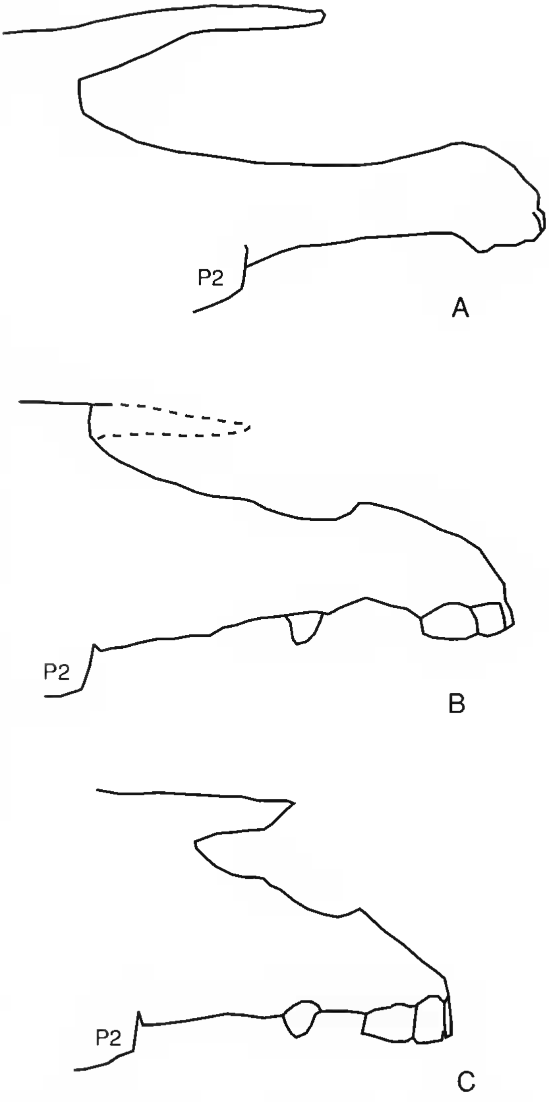

Fig. 13. — **A**, upper snout of *H. dermatorhinum*, showing deep nasal opening and long, low snout; holotype, Uppsala No. 3872, subadult (after Sölve 1927, table I: 1); **B**, upper snout of *H. moldavicum*, showing medium deep nasal opening and snout; holotype, PIN 1256/3639 (after Gromova 1952, table I 3), **C**, upper snout of *H. giganteum*, showing very short nasal opening; holotype, OGU 1015 (after Gromova 1952, table 12: 2). Drawings not to scale.

### *Hipparions with a narrow snout*

Extreme among the Asiatic hipparions with a long and narrow snout is *H. tchicoicum* Ivaniev, 1966 (Qiu *et al.* 1987, pl. XIII); the snout is narrow also in the lower jaw and the symphysis long (Fig. 12: Htc). The nasal opening is very short, ending at a level almost 2 cm in front of P2; it is short also in relation to snout length. The large preorbital fossa is evidently situated close to the orbit (orbit not visible).

*Hipparion dermatorhinum* Sefve, 1927 from China has a long snout in relation to skull length, and the snout is low and narrow (Sefve 1927, table I: 1-3; Qiu *et al.* 1987, pls XLI, XLII) (Figs 10, 11: Hd). In the lower jaw the snout is similarly narrow and the symphysis long (Fig. 12: Hd). The nasal opening is retracted, reaching level with P3, it is long also in relation to snout and skull length; the nasals are unreduced. The preorbital fossa is well-defined but shallow.

An upper snout from Sor, Tadzhikistan, shows the presence of a double preorbital fossa (Zhegallo 1978, Ris. 73). The narrow snout (Fig. 10: Sor), the nasal opening extension, and the double fossa closely resemble those in the specimen B-51 from Bazaleti.

*Hipparions lacking a preorbital fossa*

A skull (PIN 2433-360) from Kalmakpai, Kazakhstan, referred to as *H. hippidiodus* because it lacks a preorbital fossa (Zhegallo 1978, Ris. 61), has a long, narrow snout but may be laterally crushed, since a second specimen (PIN 2433-460) from the same locality has a medium broad snout (Figs 10, 11: Kp). In both specimens the nasal opening ends level with the metacone of P2. Originally *H. hippidiodus* was described from Loc. 115, Kingyang, China (Sefve 1927; Forsten 1968, pl. 3; Qiu *et al.* 1987, pl. XXXVIII); its snout is unknown.

Skulls from Khirgis Nur-2, Mongolia, called *H. mogoicum* Zhegallo (Zhegallo 1978), also lack a fossa. The snout in the measureable specimen is medium broad like in PIN 2433-460 from Kalmakpai, but shorter (Fig. 10: KN). The nasal opening reaches level with P2 mesostyle.

Chinese hipparions belonging in the species or species group *Proboscidipparion rocinantis-houfenense* (Hernandez-Pacheco)-(Teilhard & Young, 1931) with advanced, caballoid cheek teeth and lacking a preorbital fossa (see above), have a long snout in relation to skull length and the snout is narrow (Qiu *et al.* 1987, pls VI, VII; Forsten 1997, fig. 7) (Figs 10, 11: Hr); also the snout of the lower jaw is narrow (Fig. 12: Hr). The nasal opening is short, extending from 0.5 cm in front of P2, to level with P2 paracone.

There are four skulls of the two (?) species of typical *Proboscidipparion*, *P. sinense* Sefve (Sefve 1927, table VI: 22-24, VII) and "*pater*" Matsumoto, 1927 (Qiu *et al.* 1987, pls I-IV). The snout is rather short in relation to skull length and narrow (Figs 10, 11: Pp, Ps and Ps in bold). Also the symphysis is short, taking into account the size of the jaw, and the snout is narrow (Fig. 12: Ps and Ps in bold). The nasal opening is enormously retracted, extending from level with M1 metacone to M2 mesostyle, and the nasals are reduced and foreshortened. There is no fossa.

## DISCUSSION

### PHYLOGENETIC AND FUNCTIONAL CONSIDERATIONS

There are differences between local forms (species, subspecies, local populations) of hipparions for the proportions of the snout and the extension of the nasal opening, but within a local form these characters are quite stable. Characters of the snout and nasal opening occur in combination with different shapes and placement, even absence, of the preorbital fossa. Snout breadth: length proportions are not correlated with the extension of the nasal opening. How to delimit species and supraspecific groups when characters of the snout, nasal opening and nasals, and preorbital fossa are distributed mosaic-like, as are characters of the teeth and limb-bone size and proportions? What do these characters and the differences between forms signify? Do they have phylogenetic and functional significance? Which characters should be given more, which less weight when phylogenies are discussed and reconstructed? How to determine which characters are primitive, which derived, *i.e.* morphocline polarities?

The hipparions (*Hipparion*, *Proboscidipparion*

Sefve, 1927, *Neohipparion* Gidley, 1903, *Nannippus* Matthew, 1926, and *Pseudhipparion* Ameghino, 1904) can be distinguished from the ancestral merychippines on the basis of the cheek teeth in the lower jaw, particularly the lower molars. The lower molars of the merychippines retain a primitive, low double knot with little differentiated and rounded metaconid and metastylid loops, while in the hipparions the loops of the molar double knot are well differentiated, thus advanced. All Eurasian and African hipparions are true hipparions, with well-differentiated loops of the double knot of the lower molars, indicating dispersal to the Old World at a stage when the dental pattern already had become modernized.

In the hipparions, a short snout and short nasal opening could be considered primitive, since they characterize the merychippine ancestors, e.g. "*Neohipparion coloradense*" (originally of Osborn, 1918) from the early Barstovian of Boulder Quarry, Nebraska, and late Barstovian of NE Colorado (MacFadden 1984, figs 52, 54, 58, 59), and "*Cormohipparion*" *goorisi* MacFadden & Skinner, 1981 from the late Barstovian of Trinity River Pit 1, Texas (MacFadden 1984, figs 121, 123). On the other hand, if a short-broad snout in a hipparion is an adaptation to grazing, it should be considered a late, advanced character, since grazing evolved with the spread of c4 grasses about 7-5 Ma ago (Cerling *et al.* 1993). Some merychippines, although dentally primitive, already had a rather long snout, *e.g.* "*Eoequus*" *wilsoni* Quinn, 1955 (Quinn 1955, pls 10: 1-3, 11: 1-3, 12, 13), which although larger is probably closely related to "*Hipparion*" *shirleyi* MacFadden, 1984 (both are from Texas and Barstovian in age; MacFadden 1984, figs 28, 29). On the other hand, some North American hipparions or near-hipparions, although dentally advanced, retained a short snout and nasal opening, e.g. "*Neohipparion affine*" (originally of Leidy, 1869) from the late Clarendonian of Upper Miller Quarry, Nebraska (MacFadden 1984, fig. 63), "*Cormohipparion*" *sphenodus* (originally of Cope, 1885) from the Valentinian of Railway/Railroad Quarry, Nebraska (MacFadden 1984, figs 124, 126), and "*Cormohipparion*" *occidentale* (originally of Leidy, 1856) from the late Clarendonian of Gidley Horse Quarry, Texas (MacFadden 1984, figs 133, 136). The breadth of the snout in relation to snout length is not given in these horses.

The nasal opening in the North American hipparions does not extend posteriorly beyond the level of P2, but often ends at a level 1-4 cm in front of P2 (MacFadden 1984, table 1). Although in the Eurasian hipparions the nasal opening may be equally short, e.g. in early *H. primigenium*, the snout is generally longer in relation to skull length. In the *H. prostylum/schlosseri-dietrichi* group both the nasal opening and snout are short. In the Eurasian hipparions a deep nasal opening, posteriorly extending to a level beyond P2, has evolved several times and in combination with differently shaped, even absent, preorbital fossae, e.g. in the large *Hipparion* from Samos Q1-Andriano and Pikermi, in *H. proboscideum*, *H. licenti*, *H. dermatorhinum*, and *Proboscidipparion sinense*. The deep nasal opening in some hipparions has given rise to hypotheses that these horses had a tapir-like proboscis (Sefve 1927; Solounias & Dawson-Saunders 1988). In extant mammals with a lengthened nose, e.g. tapirs, elephants, saiga and dik diks, the nasal bones are foreshortened, thus allowing mobility of the nose (Macdonald 1984). In most of the known hipparions with an exceptionally deep nasal opening, the nasals are normally long. Only in some *Proboscidipparion* (*sinense* and "*pater*") are the nasals reduced in length, the nasal opening between the premaxillas is narrowly slit-like, and the upper symphysis long. Sole among the hipparions the snout in these *Proboscidipparion* does resemble that in a tapir (Sefve 1927). However, the deep nasal opening and foreshortened nasal bones in these *Proboscidipparion* also resemble those in a moose, *Alces alces* (Linnaeus, 1758), which has no proboscis but a large overhanging upper lip. Extant horses, which have a moderately deep nasal opening and long nasals, have very mobile lips. The hipparions may, to a varying degree, also have had mobile lips useful for gathering grass or browse.

In the extant horses the diverticulae nasi form blind sacks in connection with the nostrils and occupy the nasal opening (Ellenberger & Baum

1943; but see Gregory 1920). The longer and wider the nasal opening, the more room for the diverticulae. According to Gregory (1920) the diverticulae in extant *Equus* (Linnaeus, 1758) partly occupy the shallow subnasal (= preorbital) fossa. In the hipparions nasal opening extension and development of the fossa are not correlated. Well-developed and posteriorly deep in the large hipparions from Samos Q1-Adriano and Pikermi, the fossa is small and situated far from the nostrils in *H. licenti*, and is absent in *Proboscidipparion sinense* and "*pater*". The diverticulae comprise the vomeronasal organ with sensory pathways to the hypothalamus. The vomeronasal organ is believed to be involved with the "flehmen", *i.e* olfactorial tasting of feromones (Estes 1972), and with certain low vocalizations.

The generally narrow snout in Old World hipparions may have to do with these horses having been chiefly browsers or mixed-feeders (Hayek *et al.* 1991). Candidates for the grazing niche would be the broad-snouted forms in the *H. prostylum/schlosseri-dietrichi* complex and *H. antelopinum.* Eisenmann (1998) recently plotted least diastemal breadth to symphysial length in jaws of Old World hipparions. She differentiated specimens with a broad and those with a narrow jaw (Eisenmann 1998, figs 3, 4) and discussed jaw proportions and incisor morphology in relation to mode of feeding (whether grazing or browsing). With a few exceptions her diagrams correspond to mine, plotting lower snout width to symphysial length. The exceptions are specimens probably wrongly identified, e.g. in her figure 3 No. 7, 8 are evidently *H. verae* not *giganteum*, and No. 9 is not *H. mediterraneum.*

## TAXONOMIC CONSIDERATIONS

In hipparion taxonomy and phylogeny, the preorbital fossa is often given more weight than other characters, sometimes even at the near exclusion of other characters (see Eisenmann *et al.* 1987). Solely on the alleged resemblance of the fossa, the narrow-snouted *H. gettyi* (= *H. tudorovense*?) and *H. campbelli* (= *H. urmiense*?) with a long nasal opening are said to be the ancestor and descendant, respectively, of the short and broad-snouted *H. prostylum* with a short nasal opening (Bernor *et al.* 1996). The members in the *H. prostylum/schlosseri-dietrichi* group are believed to have given rise to hipparions lacking a preorbital fossa, although there are no signs that the fossa did disappear in this group. *Hipparion hippidiodus/platygenys* from Tarakliya, the earliest known hipparion lacking a fossa, has a medium broad snout and is of the same age as the members in the former group, while the hipparions from Khirgis Nur-2 and Kalmakpai, also lacking a fossa, may be younger. Their nasal opening is deep and long. On the supposed similarity of the fossa the long-snouted, large hipparion from Samos Q1-Andriano, with a deep and long nasal opening, is referred to as *H. giganteum* (Bernor *et al.* 1996), the type form of which has a very short nasal opening. On the other hand, *H. macedonicum* is believed to represent a species different from *H. matthewi* (Koufos 1986; Bernor *et al.* 1996), although identical to that species in skull and jaw morphology, metapodial size and proportions, and in protoconal length and plication count of its teeth. Some of these conflicting identifications seem to have been dictated by the presumed stratigraphic position of the find, rather than by its morphology. However, stratigraphic position is not a taxonomic character.

## HIPPARION MULTIPLE DISPERSAL?

Old World Hipparion has been thought to represent multiple dispersals from North America. This idea was also based on preorbital fossa morphology, ignoring the morphology of the cheek teeth and snout, and the faunal evidence against multiple equid dispersal. In the Miocene the North American equid fauna was diverse, comprising anchitheriines, para-merychippines, pliohippines, and hipparions, often several genera of each group in the same faunas (Forsten 1989). Of the anchitheriines only *Anchitherium* v. Meyer, 1834 dispersed to the Old World, none of the para-merychippines or pliohippines made it, and there is no evidence that more than one hipparion successfully crossed the Bering intercontinental connection. None of the typical North American hipparionid (sub)genera *Pseudhipparion*, *Neohipparion*, or *Nannippus* has ever been found in the Old World. Neither has any of the several Eurasian hipparions with a deep nasal opening ever been found in North America.

## CONCLUSIONS

It is dangerous to base hipparion taxonomy, systematics and phylogeny, and hypotheses about intercontinental dispersal, on single characters, *e.g.* on the preorbital fossa alone (Eisenmann *et al.* 1987). Skulls are rare, most fossil samples consist of isolated teeth and limb bones, which in multispecies samples may be difficult/impossible to objectively couple with the skulls or identify to species. The more characters that are taken into account, the more difficult is the delimitation of species and lineages, because of the mosaic combination of characters (see also Eisenmann 1998). I believe that genera of equids should be characterized on their cheek teeth, particularly on the cheek teeth of the lower jaw. Within a genus occur subgroups (species groups, in some cases worthy of subgeneric separation), which sometimes can be circumscribed on several characters in common, *e.g.* plication count of the upper cheek teeth, proportions of the limbs, preorbital fossa morphology, and snout proportions. Many finds cannot be placed within a single subgroup, as they share characters with several. There is no reason why the preorbital fossa should have priority in determining subgroup membership, but neither has any other character. Reference to species or species group should be based, if possible, on the holomorph of the find.

Stratigraphic provenance is not a taxonomic character. Stratigraphic schemes, using species of fossil horses as markers, should be regarded with suspicion. More often than not they are idealized and do not truly reflect the time range of the fossil species, which often occur at an earlier date and/or survive for a longer time than presupposed by the schemes. Subjective "morphological trends", often consciously or unconsciously constructed to fit and/or to support alleged stratigraphic successions, are equally suspicious.

Fossil equids should not be forced to fit a stratigraphy, but should be objectively interpreted against the background of stratigraphy.

**Acknowledgements**

My sincere thanks are due the curators and caretakers of the fossil collections studied for this paper (see Appendix). I also thank Dr. V. Eisenmann and an anonymous reviewer for useful comments on the manuscript.

## REFERENCES

Bernor R. L. 1985. — Systematics and evolutionary relationships of the hipparionine horses from Maragheh, Iran (late Miocene, Turolian age). *Palaeovertebrata* 15 (4): 173-269.

Bernor R. L., Koufos G. D., Woodburne M. O. & Fortelius M. 1996. — The Evolutionary History and Biochronology of European and Southwest Asian Late Miocene and Pliocene Hipparionine Horses: 307-338, *in* Bernor R. L., Fahlbusch V. & Mittman H.-W. (eds), *The Evolution of Western Eurasian Neogene Mammal Faunas.* Columbia University Press, New York, 487 p.

Bunnell F. L. & Gillingham M. P. 1985. — Foraging behaviour: Dynamics of Dining Out: 53-79, *in* Hudson R. J. & White R. G. (eds), *Bioenergetics of Wild Herbivores.* CRC Press Inc., Boca Raton, Florida, 314 p.

Cerling Th. E., Wang Y. & Quade J. 1993. — Global ecologic change in the late Miocene: expansion of $C_4$ ecosystems. *Nature* 361: 344-345.

Dompierre H. & Churcher C. S. 1996. — Premaxillary shape as an indicator of the diet of seven extinct Late Cenozoic New World camels. *Journal of Vertebrate Paleontology* 16 (1): 141-148.

Eisenmann V. 1998. — Folivores et tondeurs d'herbe : forme de la symphyse mandibulaire des équidés et des tapiridés (Perissodactyla, Mammalia). *Geobios* 31 :113-123.

Eisenmann V., Sondaar P., Alberdi M.-T. & De Giuli C. 1987. — Is horse phylogeny becoming a playfield in the game of theoretical evolution? *Journal of Vertebrate Paleontology* 7 (2): 224-229.

Ellenberger W. & Baum H. 1943. — *Handbuch der vergleichenden Anatomie der Haussäugtiere.* Aufl. 18. Berlin.

Estes R. D. 1972. — The role of the vomeronasal organ in mammalian reproduction. *Mammalia* 36: 315-341.

Forsten A. 1980. — *Hipparion proboscideum* Studer from Romania. *Annales Zoologici Fennici* 17: 159-160.

— 1983. — The preorbital fossa as a taxonomic character in Old World *Hipparion*. *Journal of Paleontology* 54 (4): 686-704.

— 1989. — Horse diversity through the ages. *Biological Reviews* 64: 279-304.

— 1997. — Caballoid hipparions (Perissodactyla, Equidae) in the Old World. *Acta Zoologica Fennica* 205: 27-51.

Forsten A. & Garevski R. 1989. — Hipparions/ Mammalia, Perissodactyla/from Macedonia/ Yugoslavia. *Geologica macedonica* 3 (2): 159-206.

Forsten A. & Krakhmalnaya T. 1997. — The hipparions (Mammalia, Equidae) from the late Miocene of Cherevichnoe on the northern Black Sea coast, Ukraina. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* 8: 489-499.

Gabuniya L. K. 1959. — *Histoire du genre* Hipparion. Transl. from Russian by J. de Saint-Aubin and J. Roger, Bureau de Recherches Géologiques et Minières, Trad. n° 2696, 515 p.

Gregory W. K. 1920. — Studies in comparative myology and osteology, V. On the anatomy of the preorbital fossae of Equidae and other ungulates. *Bulletin of the American Museum of Natural History* XLII: 265-284.

Gromova V. I. 1952. — Gippariony (Rod. *Hipparion*). *Trudy Paleontologicheskogo Instituta, Akademii Nauk SSSR* 36: 475 p. [in Russian].

Hayek L.-A. C., Bernor R. L., Solounias N. & Steigerwald P. 1991. — Preliminary studies of hipparionine horse diet as measured by tooth microwear. *Annales Zoologici Fennici* 28 (3-4): 187-200.

Koufos G. D. 1986. — Study of the Vallesian hipparions of the Lower Axios valley (Macedonia, Greece). *Geobios* 19: 61-79.

— 1987a. — Study of the Turolian hipparions of the Lower Axios Valley (Macedonia, Greece). 1. Locality "Ravin des Zouaves-5" (RZO). *Geobios* 20 : 293-312.

— 1987b. — Study of the Pikermi hipparions, Part I-II. *Bulletin du Muséum national d'Histoire naturelle*, Paris, série 4, C 9 (2-3) : 197-252, 327-363.

— 1988. — Study of the Turolian hipparions of the Lower Axios Valley (Macedonia, Greece). 4. Localities of Dytiko. *Palaeovertebrata* 18 (4): 187-239.

Macdonald D. (ed.) 1984. — *The Encyclopedia of Mammals. 2.* Equinox Ltd., Oxford.

MacFadden B. J. 1984. — Systematics and phylogeny of *Hipparion*, *Neohipparion*, *Nannippus*, and *Cormo-hipparion* (Mammalia, Equidae) from the Miocene and Pliocene of the New World. *Bulletin of the American Museum of Natural History* 179 (1), 195 p.

Matthew W. D. 1929. — Critical observations upon Siwalik mammals. *Bulletin of the American Museum of Natural History* LVI: 427-460.

Meladze G. K. 1967. — *Gipparionovaya fauna Arkneti i Bazaleti*. Izdat. "Metsniereva", Tbilisi, 159 p. [in Russian].

Nikolov, I. 1971. — Neue Vertreter der Gattung *Hipparion* in Bulgarien. *Bulletin of the Geological Institute, Bulgarian Academy of Sciences*, Ser. Paleontol., 20: 107-122 [in Bulgarian, with German summary].

Qiu Z., Huang W. & Guo Z. 1987. — The Chinese hipparionine fossils. *Palaeontologia Sinica*, N.S. C, 25: 250 p. [in Chinese, with English summary].

Quinn J. H. 1955. — Miocene Equidae of the Texas Gulf Coastal Plain. *University of Texas Publications* 5516: 102 p.

Sefve I. 1927. — Die Hipparionen Nord-Chinas. *Palaeontologia Sinica*, Ser. C, IV (2): 91 p.

Solounias N. & Dawson-Saunders B. 1988. — Dietary adaptations and paleoecology of the late Miocene ruminants from Pikermi and Samos in Greece. *Palaeogeography, Palaeoclimatology, Palaeoecology* 65: 149-172.

Solounias N. & Moelleken S. M. C. 1993. — Dietary adaptation of some extinct ruminants determined by premaxillary shape. *Journal of Mammalogy* 74 (4): 1059-1071.

Sondaar P. Y. 1971. — The Samos *Hipparion*. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, Ser. B, 74 (4): 417-441.

Watabe M. & Nakaya H. 1991. — Cranial skeletons of *Hipparion* (Perissodactyla, Mammalia) from Maragheh (Turolian, Late Miocene), Northwest Iran. *Memoirs of the Faculty of Sciences*, Kyoto University, Ser. Geology & Mineralogy, LVI (2): 55-125.

Zhegallo V. I. 1978. — Gippariony Tsentralnoi Azii. *Sovmestnaya Sovetsko-Mongolskaya Ekspeditsiya, Trudy* vyp. 7: 1-152 [in Russian].

Zouhri S. 1992. — *Hipparion molayanense* n.sp. (Perissodactyla, Equidae) du Turolien de Molayan (Afghanistan) et un nouvelle typologie des Hipparions turoliens de l'Ancien Monde. *Comptes Rendus de l'Académie des Sciences*, Paris, série II, 315 : 1555-1560.

— 1996. — Un nouvel equidé, *Hipparion molayanense* nov.sp., dans le gisement Turolien de Molayan en Afghanistan. *Geobios* 29 (4) : 437-454.

*Submitted for publication on 2 April 1998;*
*accepted on 31 July 1998.*

## APPENDIX

List of hipparion specimens used in this paper. Listed are only specimens, which have yielded measurements on the upper and/or lower snout. Listed are not specimens lacking or with fragmentary snout, although representing the same species, from the same localities, and present in the same collections. When studied in the 1960-ties, most collections were still inadequately filed, as reflected by the frequent lack of collection numbers.

***Hipparion*** sp.
(with double preorbital fossa), not named.

Locality. — Samos Q1 (and Q5?) and Samos without exact locality data.

Age. — Turolian.

Materials. — Samos: (AMNH 20628, probably 20599, 22908, 94905 & no No., all Q1) five skulls, (AMNH 94906 & no No., Q1) skull and jaw, possibly also (AMNH 20786 & 22912, Q5); (SMF no No. and possibly no No.) two jaws; Geological Museum, Lausanne (No. 151, 610, 843, Andriano) three jaws; Carnegie Museum, Pittsburgh (No. 2126) a jaw.
*H. matthewi* or *H.* sp (with a double fossa): Samos (AMNH 22928, Q5) jaw; (SMF no No.) two jaws; (MNHN 1955-1 73) a jaw.
*H.* sp. (with double fossa) or *H. schlosseri-dietrichi*: Samos (AMNH 20651, 20721 & no No., Q1; No. 10733) four jaws; Geol. Mus., Lausanne (Nos. 78 & 1031, Andriano) two jaws; Nat. Hist. Mus., Vienna (1911 V 135) a jaw.

***Hipparion*** sp.
not named, not *H. mediterraneum*.

Locality. — Piera, Spain.

Age. — Turolian.

Materials. — Institut Paleontologic Dr. M. Crusafont, Sabadell (IPS.P 6359, 6360, 6365, 6372, and two specimens without a readable number) skulls.

***Hipparion africanum*** Arambourg, 1959

Type locality. — Oued el Hammam, Algeria.

Age. — Vallesian.

Materials. — (MNHN 141 & no visible No.) two skulls, (MNHN 89, 98, 143) three jaws.

***Hipparion antelopinum*** Falconer & Cautley, 1847

Type locality. — Potwar Plateau, Siwaliks, Pakistan.

Age. — Turolian.

Material. — (AMNH 19761) a skull.

***Hipparion brachypus*** Hensel, 1862

Type locality. — Pikermi, Greece.

Age. — Turolian.

Materials. — Pikermi: British Museum of Natural History, London (BMNH unreadable No.) skull, (BMNH 11211, 11213 & 11217) three jaws; (MNHN no No.) skull, (MNHN 31 & three specimens without a number) four jaws; Geological Institute, Göttingen (no No.) skull; Swedish Museum of Natural History, Stockholm (no No.) jaw; Humboldt Museum, Berlin (no No.) skull; Yale Peabody Museum of Natural History (No. 11768) skull with jaw.
In addition: Natural History Museum, Basel (PK 89) a jaw of either *H. brachypus* or *H. mediterraneum*.
*H.* aff. *brachypus*: Samos: (AMNH 22838, Q4) a skull, possibly (AMNH 22912 & 22922, Q5); (SMF 4707) a skull, (SMF no No.) a jaw; Geol. Inst., Budapest (OK 425) a jaw; Nat. Hist. Mus., Vienna (No. 1911 V 118) a skull: Geol. Inst., Lausanne (No. 73 & 148, Andriano) skull & jaw, (No. 175, Andriano) a jaw; Hessisches Landesmuseum, Darmstadt (Ss 45) a jaw. — Beluska, Macedonia (former Yugoslavia): Prirodnjacki Muzej, Beograd (PM 2791) jaw. — Karaslari, Macedonia: (PMM 193/73) jaw. — Maragheh, Iran: (MNHN 561) a jaw.
*H.* aff. *brachypus* or *H. proboscideum*: Samos: (AMNH 20640, Q1) a jaw; Inst. of Geol. & Paleontol., Münster (SI/no No.) a jaw.

***Hipparion catalaunicum*** Pirlot, 1956

Type locality. — Hostalets de Pierola, Spain.

Age. — Vallesian.

Materials. — (BMNH 16397, type *H. catalaunicum*) a skull.

***Hipparion dermatorhinum*** Sefve, 1927

Type locality. — Loc. 30, Bao De, Shanxi, China.

Age. — Turolian.

Materials. — Loc. 30: Paleontol. Inst., Uppsala (M 3872, type) skull. — Huang Lu Kou, China (AMNH 41-L 310) skull and jaw. — Bao De, Shanxi, China: (IVPP no No.) skull and jaw, (IVPP 8243?) skull and jaw, (IVPP no No.) jaw.

### ***Hipparion elegans*** Gromova, 1952

Type locality. — Pavlodar, Kazakhstan.

Age. — Turolian.

Materials. — (PIN no visible No.) a skull, (PIN 2346-2479, -2516, -4883, 2413-2847, -2864) five jaws.

### ***Hipparion garedzicum*** Gabuniya, 1959

Type locality. — Udabno, Georgia.

Age. — Late Vallesian-Early Turolian.

Materials. — Musei Grusii, Tbilisi (156/13 type *H. garedzicum* & 270/34) two skulls.

### ***Hipparion giganteum*** Gromova, 1952

Type locality. — Grebeniki, Moldova.

Age. — Early Meotian/Late Vallesian/Early Turolian.

Materials. — (OGU 1012/2, 1015 type & 1017) three skulls, (OGU 1018) skull and jaw, (OGU unreadable No.) a jaw.
In addition OGU 908, a skull, is intermediate between *H. verae* and *H. giganteum*.

### ***Hipparion hippidiodus*** Sefve, 1927

Type locality. — Loc. 115, King Yang Hsien, Gansu, China.

Age. — ?Turolian.

Materials. — Kalmakpai, Kazakhstan: (PIN 2433-340, -360, -340) three skulls.

### ***Hipparion licenti*** Qiu, Huang & Guo, 1987

Type locality. — Sianhotsun, Tchangkou, Yushe, Shanxi, China.

Age. — Ruscinian.

Material. — (BMNH 44577, cast F:AM 125708) skull.

### ***Hipparion matthewi*** Abel, 1926

Type locality. — Samos without exact locality data.

Age. — Late Vallesian to and including Turolian.

Materials. — Samos, Greece: (AMNH 22907 & 22936, Q5) two skulls, (AMNH no No., Q5) a jaw; (SMF 4710 & no No.) two skulls, (SMF no No.) a jaw; Nat. Hist. Mus., Vienna (no No.) a skull; British Museum of Natural History, London (BMNH 14071, cast of type) skull & jaw; Geol. Inst., Budapest (OK 557, type of *H. matthewi*) skull and jaw. — Ravin de Pluie, Greece: University of Thessaloniki (RPI-21 type *H. macedonicum* Koufos & RPI-36) two jaws. — Beluska, Macedonia (former Yugoslavia): Prirodnjacki Muzej, Beograde (PM 2659/197 & 2751) two jaws.

### ***Hipparion mediterraneum*** (Roth & Wagner, 1855)

Type locality. — Pikermi, Greece.

Age. — Turolian.

Materials. — Pikermi (BMNH 11215) jaw; (MNHN no No.) skull and jaw, (MNHN 514-31 & no No.) two jaws; Nat. Hist. Mus., Vienna (no No.) a skull, (no No.) a subadult jaw; University of California Museum, Berkeley (UCM 63422) a jaw; US National Museum, Washington, D.C. (No. 267) a jaw; Swedish Museum of Natural History, Stockholm (no No.) two jaws; Geological Institute of the University, Göttingen (no No.) a jaw; Natural History Museum, Stuttgart (no No.) jaw to skull.
*H.* cf. *mediterraneum*: Bazaleti, Georgia: Institute of Paleobiology, Tbilisi (B-51) skull, (B-54) a jaw. — Maragheh, Iran: (MNHN no No.) a jaw; Nat. Hist. Museum, Vienna (no No., Ketchawa) jaw; National Museum, Praha (no No.) jaw.

### ***Hipparion mogoicum*** Zhegallo, 1978

Type locality. — Khirgis Nur, Mongolia.

Age. — Turolian.

Materials. — Khirgis Nur: (PIN 3222-193 type & no No.) two skulls.

### ***Hipparion molayanense*** Zouhri, 1992

Type locality. — Molayan, Afghanistan.

Age. — Turolian.

Materials. — (MNHN Mo 040 & 1758) two skulls.

### ***Hipparion moldavicum*** Gromova, 1952

Type locality. — Tarakliya, Moldova.

Age. — Meotian/Turolian.

Materials. — Tarakliya: Paleontological Institute & Museum, Moscow (PIN 1256-2922, -3639 type, -3647, -3648 & no No.) five skulls, (PIN 1256-3619, -3620, -3638, -3641, -3642, -3643, -3700, -4189, -4191, -6605, -6944, -7027 & four without a number) jaws. — Novoelizavetovka, Ukraine: (OGU 1233, 1306, 1307, 1313, 1314, 1459, 3369, 3371) skulls, (OGU 1394-95, 1401, 1403, 1404) jaws. — Cherevichnoe, Ukraine: Dept. Paleontol. & Paleontol. Mus., Kiev: (No. 45-2665, -3849, -3925) three skulls. — Tchobruchi, Moldova: (OGU 3081) skull, (OGU 3078) two jaws; Mus. Ordzonikidze, Moscow (No. 2080 & no No.) two jaws, (No. 2026 & 2081) a skull and jaw may be either from Tchobruchi or Grebeniki.
*H.* aff. *moldavicum*: Novaya Emetovka-2, Ukraine:

Dept. Paleontol. & Paleontol. Mus., Kiev (No. 25-2439, -2923, -3005, -3200, -3310) skulls. — Chimishlia, Moldova: Institute of Geology & Paleontology, Univ. Bucharest (No. 66/(378), 378a & no No.) three skulls, (no No.) jaw; Regional Museum, Chisnau (No. 44040/79 & -/81) jaws. — Maragheh, Iran: (BMNH 3924) skull; (MNHN three specimens without No.) three jaws; Nat. Hist. Mus. Vienna (no No., Kopran & Ketchawa) two jaws.

***Hipparion platygenys*** Gromova, 1952
(?younger synonym of *H. hippidiodus* Sefve 1927).

Type locality. — Tarakliya, Moldova.

Age. — Meotian/Turolian.

Materials. — (PIN 1256-2942, -3634 & no No.) three jaws.

***Hipparion praegiganteum*** Tarabukin, 1967

Type locality. — Chimishlia, Moldova.

Age. — Meotian/Turolian.

Materials. — Regional Museum, Chisnau (No. 4040/84, type) skull, (No. 4040/83) jaw.

***Hipparion primigenium*** (v. Meyer, 1829)

Type locality. — Eppelsheim, Germany.

Age. — Vallesian.

Materials. — Eppelsheim: Geol. Inst., Budapest (OK 22) a jaw. — Höwenegg, Germany: Humboldt Museum, Berlin (no No., cast) skull and jaw; Hessisches Landesmuseum, Darmstadt (Hö 58/VI) skull and jaw, (Hö. 54B) a jaw. — Vila de Caballs, Spain: (IPS no No.) skull and jaw. — Can Llobateres, Spain: (IPS no No.) jaw. — Inzersdorf, Austria: Natural History Museum, Vienna (SK 1346 & no No.) two skulls, (No. 1875 VI 5) a jaw. — Wienerberg, Austria: Nat. Hist. Museum, Vienna (1842 LVII 11) a jaw. — Prottes, Austria: Geological Institute, Univ. of Vienna (No. 958) a jaw. — Baltavar, Hungary: Geol. Inst., Budapest (No. 90) a jaw; Natural History Museum, Budapest (No. 319b, 390, 391) three jaws. — Nesebr, Bulgaria: Geological Institute, Univ. Sofia (No. 130) skull, (No. 40, 133 & no No.) three jaws.

***Hipparion proboscideum*** Studer, 1911

Type locality. — Samos without exact locality data.

Age. — Turolian.

Materials. — Samos: (AMNH 20771, Q1, AMNH 20772, Q1s) two skulls; (SMF 4706, 4708, 4709) three skulls; (SI/4) a skull, (possibly SI/208) a jaw; (possibly BMNH 4359) a jaw. — Ravin des Zouaves: Univ. Thessaloniki (RZO-60) skull.

*H.* sp. (cf. *proboscideum*): Cherevichnoe, Ukraine: Dept. Paleontol. & Paleontological Museum, Kiev (No. 45-2664, -4282) two skulls.
*H. proboscideum* or *H.* sp. (with double fossa), Samos: (SI/277) a jaw.

***Hipparion prostylum*** Gervais, 1849

Type locality. — Mt. Léběron, France.

Age. — Turolian.

Materials. — Faculté des Sciences, Lyon (no No.) a skull with jaw; Faculté des Sciences, Montpellier (no No.) a lower snout.

***Hipparion prostylum/H. schlosseri-dietrichi***
an entity not well defined, resembling both species.

Type locality. — None, but present in southern Macedonia (former Yugoslavia) and northern Greece, possibly also in Maragheh, Iran.

Age. — Turolian.

Materials. — Saloniki, Greece: (Coll. Arambourg & Puyhaubert) Muséum National d'Histoire Naturelle, Paris (MNHN 1919-8) two skulls, (MNHN 1911-23) a jaw. — Ravin des Zouaves, Greece: University of Thessaloniki (RZO-76, -105, -145, -154) four jaws. — Karaslari, Macedonia (former Yugoslavia): Prirodonaucen Muzej na Makedonija, Skopje (PMM 86/73, 93/73 subadult & 203/73) skulls, (PMM 410/73) a jaw.
In addition: Umen Dol, Macedonia, (PMM 99/60) a skull of either *H. matthewi* or *H. prostylum/H. schlosseri-dietrichi*. — Maragheh, Iran: (MNHN three specimens without No.) three skulls.

***Hipparion sarmaticum*** Lungu, 1973

Type locality. — Kalfa, Moldova.

Age. — Middle Sarmatian/Vallesian.

Materials. — Kalfa: Tiraspol Pedinstitut, formerly Tiraspol, now Chisnau (no No.) five jaws. — Braila, Moldova: (PIN 646-12) a skull.

***Hipparion schlosseri-dietrichi***
Antonius, 1919-(Wehrli, 1941)
Both names were given evidently the same species; Antonius' name is older, but possibly not valid (description incomplete, type not figured). Wehrli used the genus name *Hemihipparion*.

Type locality. — Samos without exact locality data.

Age. — Turolian.

Materials. — Samos, Greece: American Museum of Natural History, New York (AMNH 20596, 20598, 20608, 20692, 20997 & two without number, all Samos Q1) seven skulls, (AMNH 20603, 20650, 20655, 20667, 22787, all Q1) five jaws, (AMNH 22860, Q4 & no No., ?Q4) two skulls, (AMNH 22990, Q6) skull; Senckenberg Museum, Frankfurt (SMF no No.) three jaws; Natural History Museum, Vienna (No. 1911 V 114, type *H. schlosseri*); possibly Geological Institute, Budapest (No. 274) skull; Institute of Geology & Paleontology, Münster (SI/7, type *Hemihipparion dietrichi* & SI/28) two skulls, possibly (SI/236) a jaw; Teylers Museum, Haarlem (No. 15470 & no No.) two skulls; Geological Museum, Lausanne (No. 132) skull, (No. 84 & 195 from Samos, Andriano) two jaws; University of Texas-Austin, Bur. Econ. Geol. (No. 40275 cast of CMNH P. 12868) skull. — Maragheh, Iran: Nat. Hist. Mus. Vienna (no No., Kopran) jaw.

### ***Hipparion tchicoicum*** Ivanjev, 1966

Type locality. — Beregovaya, Russia.

Age. — Villafranchian.

Materials. — Shamar, Mongolia: (PIN 3381-53) jaw. — Peihaitsun, Matsegou, Yushe, China: (IVPP THP 19009 & 19013) skull and jaw. —Yidjouantsun, Yushe, China (IVPP THP 10302) jaw.

### ***Hipparion tudorovense*** Gabuniya, 1959

Type locality. — Tudorovo, Moldova.

Age. — Meotian/Turolian.

Materials. — (OGU 1780 type *H. tudorovense*) a skull, (OGU 906, 1783 & no No.) three jaws.

### ***Hipparion verae*** Gabuniya, 1979

(originally *H. gromovae* Gab. 1959, preoccupied by *H. gromovae* Villalta & Crusafont, 1957)

Type locality. — Grebeniki, Moldova.

Age. — Early Meotian/Late Vallesian/Early Turolian.

Materials. — Grebeniki: University of Odessa Museum, Odessa (OGU 916, 917, 1012/1 & 1016 type) four skulls, (OGU 889, 897, 898, 905, 1016, 1462 & no No.) seven jaws; Department of Paleontology & Paleontological Museum, Kiev (No. 408-47 & 408-114) two jaws; Museum Ordzonikidze, Moscow (Nos. 2027, 2051, 2079 & no No.) four jaws, (No. 2061) a skull, said to be from Tchobruchi, resembles *H. verae*.
*H.* aff. *verae*: Beluska, Macedonia (former Yugoslavia): (PM 2660/196) skull, (PM 2743/195) jaw.

### ***Proboscidipparion "pater"*** Matsumoto, 1927

Type locality. — unknown.

Age. — Ruscinian-Villafranchian.

Materials. — Nihetsun, Yushe, China: (IVPP THP 20763) skull, (IVPP THP 30756) jaw. — Loc. 26, Peihaitsun, Yushe, China (IVPP THP 14312 lectotype) skull and jaw.

### ***Proboscidipparion rocinantis***
(Hernandez-Pacheco, 1921)

Type locality. — Puebla de Almoradier, Spain.

Age. — Villafranchian.

Materials. — Villaroya, Spain: (IPS 2085) a skull, (IPS V 196, unreadable No. & no No.) three jaws. — Kvabebi, Georgia: Inst. Paleobiol., Tbilisi (K-48) a skull. — Shamar, Mongolia: (PIN 970/2086) a jaw. — Peihaitsun, Matsekou, Yushe, Shanxi, China: Institute of Vertebrate Paleontology & Paleoanthropology, Beijing (IVPP THP 10331 & 10508) skull, skull and jaw, (IVPP THP 10097) a jaw. — Yinkiangtsun, Yushe, China (IVPP THP 10733) skull and jaw. — Hsi Chwang/Hsiao Chuang, Shanxi, China (AMNH 96-B 1031) skull and jaw, (AMNH 64-B 815) skull.

### ***Proboscidipparion sinense*** Sefve, 1927

Type locality. — Mien Chih Hsien, Lankou, Henan, China.

Age. — Villafranchian.

Materials. — Mien Chih Hsien: Paleontological Institute, Univ. Uppsala (M 3925 & 3926 type) skull and jaw. — Yushe, Shanxi, China: Beijing Natural History Museum (no No.) skull and jaw.